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HEREDITY OF HAIR COLOR IN MAN

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INTRODUCTION

Types of Hair Color.—The heredity of hair color in mammals is a subject of great complexity, not to be lightly entered upon. It is a subject in which much knowledge has been gained in recent years through the work of Bateson and his associates, Castle and his pupils, Cuenot and others. Nevertheless certain important points remain uncertain. First, and fundamental for our purpose, is the question of the number of factors involved in any hair color. All are agreed that there is a special red pigment (a lipochrome) that stains the hair diffusely. In clear red hair one sees, in sections, a yellowish red tinge that is not bound up with any structures. With a high power one sees elongated, spindle-shaped bodies, which are apparently the remains of nuclei and are devoid of granules. In all other hair (except that of albinos) one sees granules grouped in the spindle-shaped bodies. In black hair (Chinaman, Fig. A) these granules are large and numerous in each group (average, 12) and appear of a dark brown color. In very dark brown hair (negro, Fig. B) the granules are perhaps a little larger but much less numerous in each group (average, 6); and the color is a much less intense brown. In hair of a cold, mouse brown (Fig. C) (about No. 25 in

E. Fischer's hair scale¹) the granules are small, very few in each group (average 4) and slightly colored. The dark red hair of the orangutan is due chiefly to granules whose color is well reproduced by sepia on a clear background; but in the head hair of the golden baboon, which is striped golden and black, much diffuse golden pigment is found and (in the black zones) dark sepia granules of



FIG. A. $\times 1150$.
CHINAMAN.

FIG. B. $\times 1150$.
LEON M. (NEGRO).

FIG. C. $\times 1150$.
MOUSE-BROWN. "A."

medium size and frequency. In twoscore preparations of the hair of man and primates we have not found in any instance jet-black granules such as are characteristic of black mice. In our preparations, many of which are thin sections kindly cut for us by Miss Lutz, the granules vary in size, number and intensity, but there is no discontinuity between the lighter and darker sepia pigments; and, as stated, we have not found a coal black hair either in Chinese, Japanese, Indian, Negro or Italian, and not even in the black spider monkey. There is an interesting parallel case in poultry where even in the Black Minorcas and the Black Cochins the pigment is a dense sepia brown. We conclude, therefore, that such discontinuous color types as are described in domesticated animals such as

¹ Made by Franz Rosset, Freiburg i/Br. See E. Fischer, *Korrespondenz. Blatt, Deutsch. Gesell. f. Anthropologie, Ethnologie u. Urgeschichte*, XXXVIII, 141-147. September-December, 1907.

fancy mice and guinea pigs under the names of yellow, chocolate and black are not fundamentally distinct, but have probably been made so in the process of perfecting the standard groups. Indeed, a casual acquaintance with the variety of human hair color as one meets with it in the streets of any large city shows that there are all intergrades between yellow, light brown, dark brown and black hair and even the reds pass (through dark red and red brown) into the warm browns. It may consequently be concluded, at least provisionally, that there are two main types of pigment in human hair; a reddish yellow, which finds its intensest development in bright red, and a sepia brown whose intensity varies from a light yellow to dark brown and black. Finally, the two pigments may be combined² and in such cases the brown pigment may quite obscure the red.

The conclusion here reached concerning the factors involved in human hair color are not, we fear, in accord with the recent investigations on other mammals. They rather speak against the theory of well-developed unit characters in human hair pigment. Brown and black colors there are and an intensifier or a diluter; on the other hand, these are not well defined units but occur in all conceivable degrees. The facts of intensity in human hair color indicate that the absence of selection made on the basis of intensity has resulted in the blending of color unit characters or has not afforded the selective means by which they have elsewhere been formed.

General Scheme of the Tables.—The data concerning a single family are placed in one line. At the extreme left are given certain reference letters by which the family is designated. Then follow the number of children in the designated family that have hair of the class named at the top of each column. The following six columns give the color of the hair of the mother (M), father (F), mother's mother (MM), mother's father (MF), father's mother (FM) and father's father (FF) so far as known.

² It is clearly seen in the hair of the mother of the *Lyn* family (Table X, b).

The principal abbreviations of the names of hair colors are as follows: *br*, brown; *chest*, chestnut; *dk*, dark; *fl* or *flax*, flaxen; *gold*, golden; *lt*, light; *med*, medium; *n*, black; *v*, very; *yell*, yellow. Names of colors in parentheses () indicate juvenile condition.

Classification of the Tables.—Three series of tables may be considered. A, including cases where black or

A. HEREDITY IN ABSENCE OF BLACK OR BROWN PIGMENT IN PARENTAGE

TABLE I. DISTRIBUTION OF HAIR COLOR IN OFFSPRING WHEN NEITHER PARENT SHOWS BROWN PIGMENT

Reference Letters.	OFFSPRING.				ANCESTRY.					
	Tow.	Yell.	Gold.	Red.	M.	F.	MM.	MF.	FM.	FF.
Rit	4				flax	flax	flax	flax	flax	flax
Hak	11	2			lt. yell.	flax	"lt."	"lt."	"lt."	flax
Dex	1	4			blond	blond	blond	blond	blond	blond
Ste-E	2				gold	flax	br.	br.	lt. br.	N(flax)
Reg-A			6		gold	gold	gold	gold	gold	gold
Edw				3	dk. red	lt. red	—	—	—	—
Swe	2		1		lt. red	flax	lt. br.	dk. br.	dk. br.	dk. br.

brown pigment is absent from both parents; B, including cases when brown is present in both parents and red is not visible in either; and C, including cases where both brown and red are visible in the parentage.

B. HEREDITY OF BLACK AND BROWN PIGMENT IN PARENTAGE

TABLE II. DISTRIBUTION OF HAIR COLOR IN OFFSPRING OF PARENTS ONE OF WHOM HAS THE LEAST INTENSITY OF BROWN (FLAXEN, GOLDEN) AND THE OTHER A SLIGHTLY GREATER INTENSITY OF BROWN (LT. BR.)

Reference Letters.	OFFSPRING.				ANCESTRY.					
	Flax.	Yell.	Yell.-Br.	Lt. Br.	M.	F.	MM.	MF.	FM.	FF.
Boy-A	2				flax	lt. br.	lt. br.	blond	lt. br.	lt. br.
Hal-A	1	2	1		lt. br.	flax	N.	lt. br.	flax	flax
Deg	1	1			lt. yell.	lt. br.	br.	dk. br.	lt. br.	lt. br.

The foregoing 7 families, comprising 36 children, illustrate a simple case. When both parents lack the brown pigment the children will all lack it. When the diffuse

pigment has a weak intensity in the parents it will have the same character in the children; but where it has a strong intensity, as red, in the parents it may have the strong intensity in some (Swe) or all (Edw) of the children.

As compared with Table I, Table II shows a greater variation in the offspring—the classes light brown and yellow brown make their appearance and comprise just 50 per cent. of the offspring, a result that accords with the hypothesis that light brown is heterozygous and flaxen or light yellow is recessive, for, $DR \times RR$ is expected to yield 50 per cent. of the DR (light brown) type. We note here as in Table I that the hair is in no case darker in the children than in the darker parent; but it may be less dark.

TABLE III. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN BOTH PARENTS HAVE LIGHT BROWN HAIR

Reference Letters.	OFFSPRING.				ANCESTRY.						
	Flax.	Go.B.	Yell.-Br.	Lt. Br.	Auburn.	M.	F.	MM.	MF.	FM.	FF.
Byr	3	1	1	2?		Lt. br.	Lt. br.	dk. br.	N.	Lt. br.	br.
Klo	2	1		1		Lt. br. (fl.)	Lt. br. (fl.)	Lt. br. (fl.)	N.	"lt."	br.
Pla-B				6		Lt. br.	Lt. br.	Lt. br.	Lt. br.	N.	N.
Ste-G				2		Lt. br.	Lt. br.	br.	Lt. br.	br.	—
Tuc				2		Lt. br.	Lt. br.	Lt. br.	N.	dk. br.	gold
Totals	2	4	1	11	2?						

Assuming two cases of "auburn brown" in Byr family to be essentially golden brown (this hair has not been seen by us) it appears that when both parents have light brown hair either all of the children are of the same type (Pla-B, Ste-G, Tuc. families) or else of the light brown and lighter (yellow brown to flaxen—Byr?, Klo. family). In the first case the parents act like homozygous dominants toward the lighter types; in the second case like heterozygous dominants.

In this case we obtain a total of 42 offspring, 16, or 38 per cent., dark brown and brown, and 26, or 62 per cent., light brown or lighter. Taking dark brown as hetero-

TABLE IV. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN ONE PARENT HAS DARK BROWN HAIR AND THE OTHER LIGHT BROWN

(a) *The Darker Parent Produces "Light" Germ Cells as well as "Dark."*

Reference Letters.	OFFSPRING.					ANCESTRY.							
	Flax.	Yell.	Yell.-Br.	Gold.	Lt. Br.	Br.	Dk. Br.	M.	F.	MM.	MF.	FM.	FF.
Bri				4	1			dk.br.	lt.br.	lt.br.	dk.br.	dk.br.	flax
Dou-A			1	2	2	1	1	dk.br.	lt.br.	lt.br.	dk.br.	dk.br.	lt. br.
Dou-B							3	lt.br.	dk.br.	dk.br.	lt.yell.br.	dk.red	N.
Fir	1			3				lt.br.	dk.br.	br.	br.	dk.br.	
Loc-B	2							dk.br.	lt.br.	yell.-br.	dk.br.	lt.br.	yell.-br.
Loe				4				dk.br.	lt.br.	lt.br.	N.	dk.br.	dk.br.
Mat-B					2			lt.br.	dk.br.	br.	dk.br.	lt.br.	dk.br.
Mor-A					2			dk.br.	lt.br.	lt.br.	dk.br.	dk.br.	N.
Ran-B			3	3	3			dk.br.	lt.br.	lt.br.	br.	br.	lt. br.
Sho			1		2			dk.br.	lt.br.	lt.br.	lt.red	dk.br.	br.
Totals		1	3	1	21		5	10	1				
						26				16			

zygous and dominant to light, expectation is 50 per cent. of the offspring as dark as or somewhat less dark than the darker parent and 50 per cent. light. The observed frequencies are of the expected order.

(b) *The Darker Parent is not Known to be Heterozygous in Hair Pigment.*

Reference Letters.	OFFSPRING.					ANCESTRY.						
	Flax.	Gold.	Lt. Br.	Br.	Dk. Br.	M.	F.	MM.	MF.	FM.	FF.	
Bin			1	2		dk. br.	lt. br.	dk.br.	N.	br.	dk. br.	
Fis		3			1	dk.br.	lt. br.	dk.br.	dk.br.	lt. br.	lt. br.	
Fri		2			1	dk.br.	lt. br.	br.	N.	br.	blond	
Gil-B	1		2		1	dk.br.	lt. br.	dk.br.	dk.br.	lt. br.	lt. br.	
Gue	2			2	1	lt. br.	dk. br.	dk. br.	N.	dk. br.	N.	
Hal-E			1	2	2	dk.br.	lt. br.	br.	br.	N.	lt. br.	
Huf	1	2	2		2	lt. br.	dr. br.	lt. br.	dk. br.	dk. br.	dk. br.	
Lat-A			2		1	v. dk. br.	lt. br.	N.	N.	N.	N.	
Pot			2		2	dk. br.	lt. br.	dk. br.	dr. br.	dk. br.	dk. br.	
Rog-B			3		1	dk. br.	lt. br.	dk. br.	dk. br.	N.	lt. br.	
Sin					2	lt. br.	dk. br.	lt. br.	—	"dark"	dk. br.	
Sne			2			lt. br.	dk. br.	lt. br.	dk. br.	dk. br.	N.	
Wil-D		1	1	2	2	lt. br.	dk. br.	lt. br.	lt. br.	dk. br.	N.	
Totals		4	3	21	8	14						
						28		22				

In this case we obtain in a total of 50 offspring, 22, or 44 per cent., dark brown and brown and 28, or 56 per cent.,

light brown or lighter. Were the dark brown parents truly homozygous in hair color, and did the hair color of the offspring not grow darker with age, Mendelian expectation would be 100 per cent. dark brown. Actually, the result falls far short of that, just as the necessary conditions are far from being met. It is highly probable that in some of these families (notably Gil-B, Gue and Huf, and probably also Lat-A and Wil-D) the darker parent actually forms germ cells that lack black pigment. Of the four lightest haired children the ages of three that are known are 8, 10 and 15 years—ages at which the adult color is not fully shown. Under these circumstances one can not predict with certainty the outcome of matings of this class. One can only say that the proportions of light brown children and those with lighter hair should be less in proportion to the darker haired children in class B than in class A. The actual proportions in the two classes are in the direction of this expectation.

TABLE V. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN ONE PARENT HAS BLACK HAIR AND THE OTHER LIGHT BROWN HAIR
(No Division, on Account of Fewness of Families)

Reference Letters.	OFFSPRING.					ANCESTRY.							
	Flax.	Yell. Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	M.	F.	M.M.	M.F.	F.M.	F.F.
Car-B				1	3	1		N.	lt. br.	br.	N.	lt. br.	lt. br.
Dey				3				N.	lt. br.	dk. br.	N.	br.	N.
Dra		1	1					N.	lt. br.	dk. br.	N.	dk. br.	dk. br.
Jem			2		1			N.	lt. br.	lt. br.	N.	dk. br.	lt. br.
Ski		1	2	2				lt. br.	N.	"fair"	br.	N.	N.
Ser				2				N.	lt. br.	dk. br.	"light"	lt. br.	N.
Spr			1	1	1	1		lt. br.	N.	—	—	—	—
Str-B		2	1	3				lt. br.	N.	N.	lt. br.	lt. br.	—
Tre				2	1			N.	lt. br.	N.	dk. br.	—	—
Totals		2	3	1	15	5	6	1					
		<u>21</u>			<u>12</u>								

Assuming what is probably true for all the families, that the black-haired parent produces an equal number of germ cells with a tendency toward lighter hair and toward black, we should expect an approach toward an equality

of light and dark haired offspring. Actually, the lighter colors are in excess—a result again doubtless due to the

TABLE VI. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN ONE PARENT HAS BLACK HAIR AND THE OTHER BROWN HAIR

Reference Letters.	OFFSPRING.					ANCESTRY.					
	Flax.	Gold.	Lt. Br.	Br.	Dk. Br.	M.	F.	M.M.	M.F.	F.M.	FF.
Blo-A		3	2			N.	br.	—	—	—	—
Cas	1	1				N.	br.	br.	N.	flax	N.
Clu-A			3			br.	N.	—	—	—	—
Clu-B		1	1		1	br.	N.	—	—	—	—
Col-C	1	1	2	1		br.	N.	lt. br.	N.	dk. br.	lt. br.
Dru-B			3			N.	br.	—	—	—	—
Hen		1	1	1		br.	N.	N.	br.	N.	yell.-br.
Hof	1	2				br.	N.	lt. br.	lt. br.	N.	N.
Koo	1		1			br.	N.	br.	br.	br.	br.
Lea		1	2			br.	N.	br.	br.	br.	br.
Mil-A		1	1	1		N.	br.	br.	N.	N.	br.
Ros		3	2			N.	br.	br.	br.	br.	N.
Sea			4			br.	N.	br.	br.	br.	N.
Ste-D				7		br.	N.	N.	—	—	—
Sto-B				1	1	br.	N.	br.	dk. br.	br.	N.
Ver	1		1			N.	br.	br.	lt. br.	dk. br.	N.
Totals	1	4	17	19	5	9					
			$\underbrace{22}$		$\underbrace{33}$						

relative immaturity of the children as compared with their parents.

Assuming, as in the discussion of Table V, that the blacks are heterozygous (except in the Ste-D family) we should expect an equality of dark and light haired offspring modified by preponderance of the lighter type owing to the immaturity of the average of the offspring. Actually, with brown hair and lighter there are 41 children as opposed to 7 (Ste-D omitted) with either black or dark brown hair. When we compare the proportion of the children having hair brown or darker in this Table (60 per cent.), with that in Table V (36 per cent.) we realize how much more frequent the darker classes have become with the increased darkness in the hair of the second parent.

On account of the impossibility of drawing the line between the dark and the light shades of hair and on account

of the light color of immature offspring we are able only to compare this section with that which follows.

TABLE VII. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN BOTH PARENTS HAVE DARK BROWN OR BLACK HAIR

(a) When Both Parents Probably Form Light Germ Cells and Dark in Equal Numbers

Reference Letters.	OFFSPRING.						ANCESTRY.					
	Yell. Yell.-Br. Gold. Lt. Br. Br. Dk. Br.	N.	Chest.-Br.	M.	F.	M.M.	M.F.	F.M.	F.F.			
Cam-A	1	4	3	2		N. N.	N. dk. br.	"med." N.	N. dk. br.	lt. br. lt. br.	N. lt. br.	
Can		2				N. N.	N. dk. br.	N. dk. br.	N. lt. br.	dk. br. lt. br.	lt. br. lt. br.	
Cla-A		1	3			dk. br.	dk. br.	lt. br.	dk. br.	lt. br.	lt. br.	
Cur		1	1			dk. br.	dk. br.	lt. br.	br.	lt. br.	dk. br.	
Fue	1	1	1			dk. br.	dk. br.	blond	dk. br.	dk. br.	blond	
Gla-B	1	2	2	1		N. N.	N. yell.-br.	N. yell.-br.	N. N.	N. br.	br. br.	
Gor-A	2	3	2	4		dk. br.	N.	N.	br.	N. br.	N. br.	
Had		2	1			dk. br.	N.	N.	lt. br.	br.	N.	
Har-A	1	3	3	2		dk. br.	N.	br.	br.	br.	br.	
Hem-A	1	1	1			br.	N.	N.	br.	N. yell.-br.	br.	
Mck			1	1		N. N.	N. dk. br.	br. br.	br.	N. lt. br.	br. dk. br.	
Rol		1	4	1		N. N.	N. N.	N. N.	N. lt. br.	lt. br.	lt. br.	
Sim	1		1									
Totals	3	3	3	20	5	10	10	1				
				29				35				

Assuming that the qualities of light hair color and dark hair color (or absence and presence of intensifier) segregate in parents of mixed origin expectation is that Series A would yield 75 per cent. dark haired offspring, but on account of the impossibility of drawing the line between the dark and light shades of hair and on account of the light color of immature offspring we are able only to compare this series with series b in which expectation is 100 per cent. offspring of the darker color. Actually, in series b there are 59 individuals light to 137 (or about 70 per cent.) dark while in series a only 55 per cent. are dark. A part of these light haired individuals probably result from recessive light hair color of parents and a part from immaturity.

(b) When Both Parents are not Known to Form Light Germ Cells

Reference Letters.	OFFSPRING.							ANCESTRY.					
	Flax. Yell.-Br. Gold. Lt. Br.	Br.	Dk. Br.	N.	Chest. Red.	M.	F.	MM.	MF.	FM.	FF.		
Bal	3	3				dk.br.	dk.br.	dk.br.	dk.br.	dk.br.	N.		
Bar-A	4	2				dk.br.	dk.br.	N.	N.	dk.br.	N.		
Beo-A	1	1	1	1		dk.br.	N.	lt.br.	N.		N.		
Bra-C	1		1			dk.br.	dk.br.	N.	lt.br.		dk.br.		
Bra-D		1	3	2		N.	N.	dk.br.	N.		dk.br.		
But			2	1		dk.br.	N.	N.	N.		dk.br.		
Can	2					N.	N.	dk.br.	N.	dk.br.	lt.br.		
Cap	1	3				N.	N.	N.	N.		—		
Cla-C			2			N.	dk.br.	br.	N.	lt.br.	lt.br.		
Cla-D	2	3				dk.br.	dk.br.	br.	dk.br.	br.	dk.br.		
Dav-B	2	1	1			dk.br.	N.	N.	N.	N.	N.		
Dor-B	2		2	3		N.	N.	br.	N.	N.	N.		
Fal	1	2	1	2	1	dk.br.	dk.br.	N.	N.	N.	yell.-br.		
Fie	2	1	1	1		dk.br.	N.	br.	dk.br.	dk.br.	br.		
Gar	[1] ¹	[1] ²		3		N.	N.	N.	N.	N.	N.		
Gra-A	1	1	1	1		dk.br.	dk.br.	N.	N.	yell.-br.	N.		
Gre-A			2			N.	dk.br.	N.	N.	dk.br.	dk.br.		
Gro-A		1	2			dk.br.	dk.br.	dk.br.	dk.br.	dk.br.	dk.br.		
Hed	1	2	1	1		dk.br.	dk.br.	br.	N.	N.	br.		
Hew-A	1 ³		2	2		N.	N.	N.	N.	N.	N.		
Hit	1		1			dk.br.	N.	N.	N.	N.	dk.br.	dk.br.	
How-B	1	3		2		dk.br.	N.	dk.br.	N.	—	N.		
Keh				4	1	N.	N.	N.	N.	N.	N.		
Lay	3	2				dk.br.	dk.br.	br.	br.	dk.br.	dk.br.		
Leo	1	1	1			N.	dk.br.	gold	N.	N.	dk.br.		
Lit-B	1	2				dk.br.	dk.br.	dk.br.	dk.br.	br.	lt.br.		
Los	1		2	1		N.	N.	N.	N.	br.	yell.-br.		
Mag	2		4			dk.br.	N.	dk.br.	N.	N.	dk.br.		
Meb		1	3	1		N.	N.	—	—	N.	—		
Nor	3			3		dk.br.	dk.br.	dk.br.	N.	N.	flax		
Oke		1	1		1	dk.br.	N.	br.	N.	N.	N.		
Par-B			1	2		N.	dk.br.	br.	N.	N.	N.		
Poe	1		2			dk.br.	N.	N.	yell.-br.	N.	N.		
Put		2		4		dk.br.	dk.br.	dk.br.	dk.br.	lt.br.	N.		
Ram		1		1	1	N.	N.	N.	N.	N.	N.		
Rem	1		1			dk.br.	dk.br.	dk.br.	dk.br.	dk.br.	dk.br.		
Ric-C		1		1	1	N.	N.	N.	N.	N.	N.		
Rob-B			2	1	2	N.	dk.br.	br.	N.	br.	dk.br.		
Sam-B	2	1		2		dk.br.	dk.br.	N.	N.	N.	N.		
Sel	1		1	2		dk.br.	N.	dk.br.	N.	N.	N.		
Squ	1		1	3		N.	N.	N.	N.	N.	N.		
Sto-C				2		N.	N.	N.	N.	dk.br.	N.		
Tho-D		1	1	1		dk.br.	N.	dk.br.	N.	dk.br.	N.		
Tru	1			2		dk.br.	dk.br.	dk.br.	yell.-br.	dk.br.	dk.br.		
Was			1	2	2	dk.br.	dk.br.	N.	N.	dk.br.	dk.br.		
Whe-A				5	1	N.	N.	N.	dk.br.	—	—		
Wol	1 ⁴					N.	N.	N.	N.	N.	N.		
Totals	8	2	4	1	44	30	72	31	1	3			
					59					137			

¹ 9 years old. ² 6 years old. ³ Also 3 flaxen, 5 to 10 years old. ⁴ Also 3 "blond," 1-9 years old.

C. HEREDITY OF RED AND BROWN PIGMENT

We have seen that the red series is quite independent of the yellow-brown series. Clear red-haired individuals lack black pigment themselves and can not transmit it to their offspring. This is, at least, *a priori* probable; but despite careful search we have found no case of two parents with clear red hair. One case of clear red and dark red is given in Table I., Edw family, in which all three children have red hair. We have one of dark red \times dark red parentage with the following remarkable record (as yet unchecked).

Reference Letters.	OFFSPRING.				ANCESTRY.					
	Yell.	Gold.	Brown.	Black.	M.	F.	M.M.	M.F.	F.M.	F.F.
Dey-B	1	3	1	4	dk. red	dk. red.	—	N	br.	N

We interpret this case to mean that the red is absent in some children (owing to heterozygosity of the parents) and dilute in others and here masked by black pigment.

TABLE VIII. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN ONE PARENT HAS HAIR OF A CLEAR RED COLOR; THE OTHER OF A BROWN

Reference Letters.	OFFSPRING.						ANCESTRY.					
	Flax.	Yell. Br.	Lt. Br.	Br.	Dk. Br.	N.	M.	F.	M.M.	M.F.	F.M.	F.F.
Bon					4		br.	lt. red	N.	br.	br.	br.
Bow	1	2	1	1			red	br.	N.	—	—	br.
Dig		4		1			N.	red	—	—	—	—
Hur	1	3					lt. red	lt. br.	lt. br.	dk. br.	lt. br.	dk. br.
May	[1]	1		1			lt. red	br.	lt. red	flax	yell. br.	dk. br.
Web	1	1	1	2	2	6	lt. red	N.	lt. red	N.	N.	N.
Totals	1	2	1	1	3	2						

In this table the yellow-brown series of colors predominates among the offspring over the reds. This we interpret to mean that, as the red parents are usually heterozygous in the intensity of red that they bear, we have approximately one half of the offspring without any (or only a slight) tendency toward red. Even when red

dominates over its absence it is frequently completely hidden by black or even dark brown. In consequence of the cooperation of these two causes we are not surprised to find considerably more than half of the offspring (70 per cent.) showing no red.

TABLE IX. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN THE PARENTS HAVE DARK HAIR CONTAINING HYPOSTATIC RED.

(a) Both Parents Have Hypostatic Red

Reference Letters.	OFFSPRING.								ANCESTRY.							
	Flax.	Yell.	Yell. Br.	Gold.	Lt. Br.	Br.	Dr. Br.	N	Chest.	Lt. Red.	M.	F.	M.M.	M.F.	F.M.	F.F.
Ear					1				1							
Hog-B					1	1	1				dk.br.	dk.br.	dk.br.	lt. red	dk.br.	red
Kel					1				2		dk.br.	dk.br.	chest.	N.	chest.	—
Smi-D						1	3				N.	N.	—	—	—	—
Totals					2	1	2	0	4	3	dk.br.	N.	N.	chest.	chest.	chest.

(b) Only One Parent is Known to Have Hypostatic Red.

Beo-A	2	1	2	5							N.	N.	br.	chest.	br.	N.
Dev	1		1								dk.br.	N.	lt.br.	N.	—	red
Gla-A		3	3	2							N.	dk.br.	N.	chest.	dk.br.	N.
Got	1	1		1	1						N.	N.	N.	N.	N.	red
Pat-A	1	1	4	3	1						N.	N.	red	dk.br.	N.	N.
Wan-A		1	1	1							N.	dk.br.	dk.br.	dk.red	br.	dk.br.
Wel-A	2		2	5	1						N.	dk.br.	N.	dk.red	—	dk.br.
Whe-D			1	1							N.	N.	dk.red	N.	lt.br.	N.
Woo-B				2							N.	dk.br.	dk.br.	gold	chest.	gold
Totals	2	1	1	5	12	18	11									

Tables VIII to X give data for answering the very difficult question of inheritance of red when associated with melanic pigment. The chief difficulty is due to the masking of the diffuse by the more intense granular pigment. The following results seem, despite this difficulty, established.

1. Two light-haired parents whose hair is without red will have no red-haired children (Table I).
2. When one parent only forms "red hair" gametes, while the other forms exclusively gametes containing the darker phases of melanic pigmentation, the offspring will show no red hair; *a fortiori*, if neither parent forms "red hair" gametes, no red hair will appear in the offspring. (Table IX, b; compare also Tables IV, V, VI and VII.)

TABLE X. DISTRIBUTION OF HAIR COLOR IN FAMILIES CONTAINING RED-HAIRED CHILDREN; AND THE HAIR COLOR OF THE ANCESTORS OF THESE FAMILIES

Reference Letters.	OFFSPRING.						ANCESTRY.											
	Flax.	Yell.	Yell.-Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	Chest.	Lt. Red.	Dk. Red.	M.	F.	M.M.	M.F.	F.M.	F.F.	
<i>(a) Both Parents Have Red Visible in Hair</i>																		
Edw					2	1				dk.red	lt.red	—	—	—	—	—	—	—
<i>(b) Only One Parent Has Red Visible in Hair</i>																		
Bur-B					3	1				auburn	dk.br.	auburn	auburn	dk.br.	dk.br.			
Bow						4				br.	br.-red	N.	br.	br.	br.			
Fin					1	1				dk.br.	dk.red	dk.br.	dk.br.	lt.br.	dk.br.			
Hol-D						1	1			red	dk.br.	dk.br.	br.	N.	br.			
Lyn					2	1	1	1		red.-br.	br.	chest.	br.	br.	br.			
Mur					1	1		1		dk.red	lt.br.	dk.red	N.	dk.br.	dk.br.			
Mye					1	1		2		br.	dk.red	red	br.	N.	br.			
Pad						1		4		lt.br.	dk.red	N.	N.	—	—			
Rav						1		1		dk.red	dk.br.	dk.red	—	—	—			
Wri								3		dk.br.	sandy	dk.br.	br.	sandy	br.			
Web					1	1	1	2	2	dk.red	N.	N.	br.-red	N.	N.			
Totals					2	3	5	5	1	2	0	16	6					
										18		22						
<i>(c) Neither Parent has Red Visible in Hair</i>																		
Bol					1	1				yell.-br.	N.	lt.br.	dk.br.	—	—			
Ear						1	1			dk.br.	dk.br.	v.dk.br.	br.-red	dk.br.	red			
Elt					2		1			br.	lt.br.	dk.br.	lt.br.	lt.br.	br.			
Fan					1	2	2			br.	N.	N.	N.	N.	N.			
Fra-D							2			N.	N.	—	—	—	—			
Fri-B					2	2		1?		lt.br.	lt.br.	br.	lt.br.	lt.br.	—			
Fro					1	1	1	1		lt.br.	br.	br.	lt.br.	—	—			
Gri					1	1	2	1	1	N.	br.	yell.	dk.br.	red	N.			
Had-A								2		N.	br.	N.	N.	N.	br.			
Kel								2		N.	N.	—	—	—	—			
Mcg-B						1	3	3	3	N.	br.	—	—	—	—			
Pra					1	3	2	1	1	yell.-br.	dk.br.	gold	N.	N.	dk.br.			
Ram						1	1	1	1	N.	N.	N.	N.	N.	N.			
Ric							1	1	2	N.	N.	N.	N.	N.	N.			
Soo					2	1		1	1	lt.br.	N.	br.	N.	red	N.			
Tay						1	1		1	lt.br.	dk.br.	br.	br.	br.	dk.br.			
Wal-C						2	1	3	2	br.	N.	N.	dk.br.	dk.br.	N.			
Wri-A						3	1	1	2	dk.br.	N.	dk.br.	N.	red	br.			
Totals						1	4	5	13	13	9	6	2	20	11			
										51		33						

3. When, on the other hand, both parents, though very dark, produce "red hair" gametes, about three sixteenths of the offspring will have clear red hair. (Table IX, a; the ratio is 3 in 12.)

4. Conversely red-haired children result from the union of two "red hair" gametes. If there is no black pigment to be considered all children, in such cases, will have red hair. If one parent has visible red and the other none (though probably heterozygous) then about half of the children show the lipochrome pigment and the other half the melanic pigment (Table X, *b*). If neither parent of red-haired children shows red in its (dark) hair then expectation is that only three sixteenths of the offspring will have red hair. Table X, *c*, shows only those families in which red actually occurs. Now in some families with the potentiality of red in one quarter of the offspring, but having only four or fewer children, a red-haired child may fail to occur and such a family would be excluded from the table. Such an exclusion would tend to reduce the proportion of non-red offspring in the total. Consequently instead of 86 per cent. of the offspring in Table X, *c*, being non-red, actually only 61 per cent. are such. In the families given there are numerous cases where the red haired are to the non-red haired offspring as 3 is to 13 or as nearly so as the size of the family permits. This is true of the Bal, Elt, Fro, Gri, Ram, Seo and Tay families. The other families show not unreasonable divergencies from the typical 3 to 13.

5. All results are in accord with the statement that red and black constitute two independent series; that red is dominant over no red, as the deeper shades of melanic pigment are dominant over the lighter; and that the dense granular melanic pigment tends to hide the diffuse pigment. Thus in Table VIII the gametes of the red-haired parent may be given as *n.R*; those of the brown-haired parent as *N.r*; where *N*, *n*. are abundance and sparsity of melanic pigment, respectively, and *R*, *r* presence and absence of lipochrome (red) pigment, respectively. Then the zygotes will be of the various forms: *nR* (red soma), *NR* (brown or black, red hypostatic), *Nr* (plain brown or black), *n.r*. (flaxen to light brown). The matings of Table IX, *a*, are of the order (*NR*, *Nr*, *nR*, *nr*) \times (*NR*,

Nr, nR, nn). Expectation in 12 offspring is 6.7 dark brown or chestnut, 2.3 clear red, 2.3 pure brown or black and .7 very light brown. This expectation is approximately realized in the totals. The matings of Table IX, *b*, are of the order (NR, Nr, nR, nr) \times (Nr). There is actually a total of 51 individuals and expectation in this case is 25.5 offspring with deep melanin or chestnut hair and 25.5 offspring with pure melanin pigmentation of some grade. No pure red should appear and none does occur. The matings of Table X, *b*, are of the order (NR, nR) \times (nR). They should give an equality of offspring of the two types: NnRR (melanin pigmentation with hypostatic red) and nnRR (red with little or no black). The matings of Table X, *c*, are of the order (NR, nR, Nr, nr) \times (NR, nR, Nr, nr). This should yield in a total of 73 offspring 43.9 having dark melanin pigment combined with (hypostatic) red; 14.6 with pure brown of some grade; 14.6 with pure red and 4.9 with sparse melanin pigmentation (yellow brown). The important proportional excess of the reds is explained in the last paragraph.

D. IS INHERITANCE OF HAIR COLOR AT ALL BLENDING AND CAN IT BE SAID TO CONFORM TO GALTON'S LAW?

We have seen that, despite the difficulties offered by change of hair color with age and by the masking of diffuse red pigment with brown granular pigment, inheritance in hair color can be brought into accord with the ordinary formula for alternative inheritance. But it may fairly be asked, since brown pigment is not a well-defined unit character, whether hair color may not equally conform to the blending type of inheritance. If there were blending ("as in human skin color"?") then the offspring of a dark and light should all be intermediate. Table V is important in this inquiry. If blending occurred the offspring of black and light brown should all be brown (or light brown because of immaturity) but dark browns and a black occur; so in Table VI the 9 blacks oppose the hypothesis; also in Tables VIII and

IX, *a*, the occurrence of red is not in accord with the hypothesis. Certainly there is no blending in an "all N" ancestry of red and yellow as in the Ram, Ric-C and Wol families of Table VII, *b*. The results clearly do not accord with the law of blending inheritance.

It remains to consider if inheritance of hair color follows Galton's law which states that the two parents determine 50 per cent. of the ancestry, the four grandparents together 25 per cent. and earlier ancestry altogether form the remaining 25 per cent.

Taking the 12 families of Tables X, *c*, whose grandparents are all given, we have in the parentage a total of 0 red in 24 parents; and of 5 red in 48 grandparents, or about 10 per cent. Assuming the same proportion of red in the unknown earlier ancestry, we have the total expected proportion of red in the offspring given by the sum

$$\begin{array}{rcl} 0 \div 24 \times 50 & = & 0 \\ 5 \div 48 \times 25 & = & 2.6 \\ .104 \times 25 & = & 2.6 \\ \hline & & 5.2 \text{ per cent.} \end{array}$$

Actually, there are about 40 per cent. of the red type, and, making every allowance, at least 18 per cent. are to be expected. Five per cent. certainly fits the facts very badly. We conclude, therefore, that Galton's law does not fit the facts as well as Mendel's law and that heredity of hair color is alternative.

E. THE NON-TRANSGRESSIBILITY OF THE UPPER LIMIT

While the application of the law of alternative inheritance to human hair color lacks something in ideal clearness and precision, one general rule stands out prominently. It is that in the midst of the varying degrees of intensity of the melanic pigmentation the intensity of the melanic pigmentation of the offspring never exceeds that of the more intense parent.

The general intensity relations of melanic hair pigment in parents and offspring are brought out in Table XI.

An inspection of this table shows that, in general, in

TABLE XI.

Grade of Darker Parent.	HAIR COLOR OF OFFSPRING.							Red Series.
	Flax.	Yell.	Yell. Br.	Gold.	Lt. Br.	Br.	Dk. Br.	
Flax	4							
Yell.	11	2						
Yell. br.	1	4						
Gold	2							
Lt. brown	4	1	2	5	14			
Brown	11	4	4	4	23	24	5	3
Dark brown	4	2	2	5	66	25	58	6
Black	3	4	5	8	60	37	49	40

the melanic series, the grade of intensity of hair pigmentation in the offspring does not exceed that of the darker parent. The only exceptions appear in the "brown" and "dark brown" parentage, where a small percentage of children are represented as of the next darker grade. Many more such cases were in our original records, but wherever the question was asked of the recorder whether the hair of the child, *A*, exceeded in darkness that of the darker parent, *B*, the reply was almost without exception negative. Samples of hair were asked for and these never proved darker in the children than in the parents. A common source of error lies in not disconnecting the effect of a slight grayness in the parent. In one sample of hair from a mother that was reported lighter than the daughter the gray hairs were carefully picked out, when it appeared that the natural color of the hairs of the mother and child were as like as possible. Consequently one is justified in laying no stress on the 11 children out of 600 (less than 2 per cent.) in which the hair color was returned as darker than that of the parents—particularly as despite efforts these returns could not be confirmed. It follows, then, that parents may be assured that their children will eventually have hair as dark as the darker parent or of a lighter tint, but not darker. Consequently, parents with flaxen or yellow hair will have children all alike and like themselves in this respect. But parents with black hair may have children with flaxen hair or with light brown hair

or (because of the masking qualities of black pigment) with red hair.

What is the relation of this principle to the law of alternative inheritance? The latter is only a special case of it. When characters A and B are crossed the more intense character appears in the offspring—the less intense character is recessive—the “heterozygous” children do not exceed the more intense parent. If, now, two such heterozygous persons be mated, one fourth of their offspring show the recessive condition, which by hypothesis is of a lower grade than that possessed by the parents; the remainder of the offspring may attain the grade of their parents; but they will not exceed that grade. This principle of the non-transgressibility of the upper alternative inheritance only, but also for blending inheritance—indeed, it seems to be of universal applicability.

An exception to this rule is exhibited by some heterozygous forms. The cross of a high-combed fowl and a low-combed is a fowl with one intermediate grade of comb. Two heterozygous combs in the parentage throw, *inter alia*, high combs. Not all cases of heterozygous forms constitute exceptions to this law of the non-transgressibility of the upper limit, and human hair color seems, even in the heterozygous condition, to follow the law. The workings of the principle are veiled in some cases of cryptomeric characters, *i. e.*, built up of hidden factors.

Certain important consequences flow from this principle. These one of us has pointed out in a brief communication to *Science*.³ If the progeny stands on the average in respect to a character at a lower grade than the parents then, if inbreeding is practised, the two parents of the next generation will probably have this character at a lower level than their parents and will produce children having the character less well developed than they have it themselves. If inbreeding be practised for several generations it is clear that in some, at least.

³ Vol. XXVIII. pp. 454-455, October 2, 1908.

of the children, the character in question would probably become quite degenerate. Since the note in *Science* was published we have read a paper by Feer, to which our attention was called by the title "Der Einfluss der Blutverwandtschaft der Eltern auf die Kinder."⁴ This paper comes very near to our point of view. After showing that retinitis pigmentosa and congenital deaf-dumbness are the diseases most closely associated with inbreeding the author concludes that they are not so much inheritable diseases in the usual sense as inheritable diseases of degeneration, and depend on degeneration of the embryonic ectoderm. It seems clear from such data as Feer adduces that our general thesis will hold true for many human characters—that inbreeding does not cause them to degenerate, but having a tendency to degenerate, inbreeding will prevent any recovery and, in addition, will hasten the downward tendency from generation to generation. The only way to avoid progressive degeneration is to bring in (usually necessarily from outside) blood with the tendency to produce the characteristic in a well-developed condition.

Combining now the results of the three studies on eye color and hair color and form made by us,⁵ it appears that two parents with clear blue eyes and yellow or flaxen straight hair can have children only of the same type, no matter what the grandparental characteristics were; that dark eyed and haired, curly-haired parents may have children like themselves but also of the less developed condition. In the latter case what the proportions of each type will be is, for a fairly large family, predictable by a study of the immediate ancestry.

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COLD SPRING HARBOR, N. Y.,
December 1, 1908.

⁴ Separate, Berlin, 1907; also "Jahrbuch für Kinderheilkunde," Bd. LXVI.

⁵ G. C. and C. B. Davenport, "Heredity of Eye-Color in Man," *Science*, N. S., XXVI, pp. 589-592, November 1, 1907; "Heredity of Hair-Form in Man," *AMERICAN NATURALIST*, XLII, pp. 341-349, May, 1908.

A MECHANISM FOR ORGANIC CORRELATION¹

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THE year 1909 is notable for its many historical associations. It is not only the fiftieth anniversary of the publication of "The Origin of Species," but it is also the centenary of the birth of Charles Darwin and of the publication of Lamarck's "Philosophie Zoologique." To the American its associations with Lincoln are precious memories. But it is not to these historical matters that I wish to refer. Science ever looks forward, not backward, and it is on certain modern aspects of the movements centering about the problem of evolution and especially on those connected with the name of Darwin that I wish to speak.

Although biologists have been familiar with Darwin's theory of natural selection for almost fifty years, it must be confessed that they are only at the threshold of the problem of evolution. That species have arisen by transmutation is now universally admitted, but how transmutation has been accomplished remains at present one of the unsolved riddles. The Lamarckian factors, though possible, must be set down as still unproved. Natural selection, so far as observation and experiment go, seems to play a real part in transmutation, but the extent of its application is still a matter of much uncertainty. Even the recently advanced mutation theory, on which hopes at one time ran high, is coming to assume at best a supplementary rôle. In fact it is evident that the most serious efforts of the past have failed of full accomplishment and it seems likely that the process of transformation is not exclusively dependent upon any single principle, but is of great complexity involving in all probability a consid-

¹ Read before the Boston Society of Natural History, February 12, 1909.

erable number of factors. Of these factors we are only beginning to get glimpses. I believe they will come into clearer view only as we progress in the solution of general biological problems. It is my intention to bring before you very briefly one of these lines of progress and to point out its possible bearing on the problem of evolution.

You are all doubtless familiar with the claim that Darwinism or natural selection is at best only a partial or insufficient factor in evolution. Its actual workings seem to be concerned with the elimination of only the most poorly adapted members of any stock; it is a process that is not closely enough adjusted to call forth those slight but constant differences which every systematist recognizes as the distinguishing marks of a species. To quote from a recent criticism:

Every student of systematic zoology or botany has a keen realization . . . of the fact that a majority of the distinguishing characters which he recognizes in the various species . . . that come under his eye are of a sort that reveal to him no trace of particular utility.

For this reason it is believed that these characters could not have been produced through natural selection. I hope to show you, however, that we can make the admission implied in this quotation, to the effect that specific characters are not necessarily useful, and still be able to explain their occurrence and fixity through Darwinism.

A general outline of this proposition has already been given by Plate in his consideration of correlation. According to this author the development of a specific character of no special use may take place through correlation, that is, through that unknown law of growth by which an indifferent organ may be so bound up with or related to a useful organ that it, the indifferent organ, is perfected along with the useful organ as this latter is developed or specialized through selection. In this way it is conceivable that a specific character, even though useless, may arise at least indirectly through natural selection. It is to be noted that Plate's conception of the mechanism of correlation is not detailed; in fact, he

describes this principle as an unknown law of growth. It is to this aspect of the subject that I wish to direct your attention.

Only a superficial acquaintance with organisms is needed to make one familiar with many examples of correlation. A hairy integument is always associated with mammary glands; albinism in fur and skin is accompanied with a red color in the eye; and many other examples of correlated characters might be given. The question that we have to consider is the nature of the association in correlated characters and much light can be thrown upon this, I believe, by a study of the ductless glands.

The ductless glands such as the thyroid, the suprarenal bodies and the hypophysis of the brain were originally supposed to be functionless, but recent work has shown them not only to be functional but absolutely essential to the continuance of life. The removal of the suprarenal bodies from a mammal is invariably followed by death within a few hours and the loss of the hypophysis or the thyroid is also fatal though only after a somewhat longer interval. It is thus quite evident that these organs are of vital importance and that the continuance of life is dependent upon their presence. But they are not only necessary for life; they profoundly influence the form and structure of the organism in which they occur. This is best seen in the case of the thyroid. In extreme disease of this gland or after its removal in the higher mammals, the skin thickens and thus produces a misshapen aspect in the features and the extremities, there is a tendency to the loss of hair, and the nervous organs are so affected that the animal sinks into a condition of semi-idiocy (cretinism). Thus there are not only fundamental internal changes, but the external features such as a naturalist might use in describing a species are profoundly modified. Certain external features, then, in the normal animal are correlated with the state of the thyroid and, as disease and experiment show, they fluctu-

ate with the changes in the state of this gland. Our normal skin and features are thus dependent upon the integrity of this internal organ.

The mechanism of correlation between two such organs as the thyroid and the skin has already been somewhat worked out. It is natural to suspect that this correlation is nervous, for both thyroid and skin are supplied with an abundance of nerves coming from a common central organ. But the fact that the symptoms already described as the result of the removal of the thyroid can be checked and even made to disappear by grafting into the animal that has lost its thyroid, a part of a living gland from another animal, shows conclusively that the nervous system is not concerned. The further observation that animals devoid of thyroids may be kept in normal condition by injecting thyroid juice into them or even by feeding them with fresh thyroid glands from other animals, has suggested the idea that this gland produces a substance which makes its way into the blood and is thus carried to those parts of the body where it is needed. It is through this substance that the skin is influenced in that in the absence of this material the skin suffers serious change. The mechanism of correlation between the thyroid gland and the skin, then, consists in a substance produced by the gland and carried in the fluids of the body to various organs, including the skin, whose growth and appearance is thereby modified.

Similar observations have led to a like conclusion concerning the action of the suprarenal bodies and the hypophysis. These organs, like the thyroid, produce substances that make their way into the fluids of the body and influence its structure and action in so profound a way that they are absolutely essential to its continued existence. In the case of the suprarenal bodies the active substance has been isolated and is known as adrenalin. Since these internal secretions have the power of calling forth or exciting very marked changes in the body, they have been given the general name of hormones. It would,

however, probably be a mistake to regard the production of these hormones as limited to a few organs such as the thyroids, suprarenal bodies, etc. The most recent work in this field points to the conclusion that all active organs of the body, nerve centers, muscles, glands, etc., produce hormones which in the blood probably exert extensive influences on the parts with which they come in contact, and examples of this kind are being rapidly discovered. It was formerly supposed that the secretion of the pancreatic juice, which is poured into the small intestine when the partly digested food from the stomach reaches that organ, was dependent upon a nervous signal given to the pancreas from the intestine, but it is now well established, through the brilliant work of Bayliss and Starling, that the action of the acid food on the walls of the intestine produces a hormone, called secretin, which when carried in the blood to the pancreas will cause that organ to secrete. The evidence of this lies in the fact that when a small amount of secretin is injected directly into the blood stream of a mammal, the pancreas, whose nerve supply may have been cut off, will begin to secrete without the presence of food in the intestine. Still more remarkable is the correlation between the mammary glands and the embryo in mammals. It is well known that as the time for the birth of a mammal approaches, the mammary glands of the parent grow in size and structural changes appear preparatory to the secretion of milk. This correlation between the growth of the embryo and the growth of the mammary glands can not depend upon nervous coordination, for the nerves of the embryo have no connection with those of the maternal body. The correlation depends upon a substance, a hormone, produced in the body of the embryo and transmitted to the blood of the mother, whereupon it so influences the mammary glands as to start their growth. The evidence for this lies in the fact that if the extracted juice of a rabbit embryo is injected periodically into the circulation of a virgin female rabbit, her mammary glands can be in-

duced to take on the growth characteristic of the early stages of pregnancy though she is absolutely without young.

Another important set of bodily correlations are those that exist between the reproductive glands and the secondary sexual organs such as the comb, hackles and spurs of the common male fowl. It is well known that if the genital glands of a young male fowl are removed before it has attained maturity, it will fail to perfect its secondary sexual organs and the usual external evidences of maleness may be absent. But if, as Shattock and Seligmann have shown, a small piece of a male gland is grafted into a young castrated male the comb, hackles, and spurs may develop as in a normal bird. It is, therefore, highly probable that the reproductive glands, like the ductless glands, produce hormones by which the development of the secondary sexual organs is determined.

Not only are hormones produced in the adult body, but they are very probably formed during development. Such at least seems to be the condition in the correlated growth of the vertebrate eye and its lens. As is well known, the eyeball in the vertebrate is formed around an outgrowth from the brain; the lens is developed from the skin in such a position as to fit the forming ball. This interesting correlation in position between the external lens and the deep-seated eyeball has been made clear by Lewis who has shown that when the forming eyeball of a given species of frog is covered by grafting over it skin from the abdominal region of even another species of frog, this foreign abdominal skin will begin to form a lens in an appropriate position for the underlying eyeball. Apparently the eyeball gives out a substance, a hormone, that so influences the adjacent skin that, irrespective of its source within certain limits, it forms a lens. Thus embryonic correlations may also depend upon hormones.

These numerous examples show that many organs of the body produce hormones that profoundly affect the

form and structure of many other organs, external as well as internal. And further that these hormones are in some cases absolutely essential to the continuance of life. In short we must consider the interior of every organism as exhibiting an environment to which every organ probably contributes and by which every organ is more or less influenced. The hormones of this environment are the mechanisms of correlation and by means of them one organ influences another. It is no longer necessary to describe organic correlation as an unknown law of growth. It is the dependence of one organ on another through the hormones that the influencing organ produces.

Granting this condition, it follows that natural selection may well be conceived to modify an internal hormone-producing organ, if this organ is of vital significance, and incidentally thus to establish a new internal environment that would so influence the form and external configuration of a given organism that it would be called a new species and yet none of the new external features by which this organism would be described might show the least usefulness.

RECENT ADVANCES IN THE STUDY OF VASCULAR ANATOMY¹

I. VASCULAR ANATOMY AND THE REPRODUCTIVE STRUCTURES

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It is perhaps unfortunate that the names applied to the great divisions of botanical investigation shift in their meaning from time to time, but it is inevitable. The content of a subject shifts with the men who put content into it. The morphology of to-day is not the morphology of half a century ago, either in its content or motive; or rather there are several conceptions of morphology existing side by side, some as an inheritance, and others as acquired characters. The older conception of morphology, presented, for example, in the model textbooks of Asa Gray, is one thing; and that introduced by the work of Hofmeister, which very slowly made its way into this country, is a very different thing.

This more recent morphology adds to the old knowledge of structures the relation of these structures in a scheme of phylogeny. Its importance lies not so much in the fact that it solves the perennial problem of phylogeny, as in the fact that it calls for the selection and comparison of structures throughout the plant kingdom. It takes the enormous débris of material that has accumulated and sifts it, passing over the trivial, emphasizing the important, and building up the body of knowledge into a structure that has some form. As knowledge advances, the trivial of yesterday may become the important to-day, and *vice versa*; but the building of a structure, upon any plan, is work of a higher order

¹ Papers prepared by request of the Council and read at the Baltimore meeting of the Botanical Society of America.

than the mere collection of building material, and especially stimulates further work to strengthen it or to demolish it.

In the decade we are considering there has come into the morphological camp a powerful ally. For convenience, we speak of it as vascular anatomy; but it is the application of the spirit of the new morphology, the evolutionary morphology, to the vascular system of plants. Before this reinforcement, the modern morphology was dealing almost exclusively with the reproductive structures: sporangia and sex-organs, with their associated structures. It had pressed these structures to the limit of technique, developing morphological cytology. With the vascular system brought into the morphological perspective, the first step was taken towards the inclusion of vegetative as well as reproductive structures. It now remains for some one to begin the organization of the remaining vegetative regions upon the same basis; and then morphology will have its facts fairly before it.

The history of the subject called "anatomy" serves well to illustrate the spirit of modern morphology. It applied to such a mass of facts as are brought together, for example, in DeBary's "Comparative Anatomy of Phanerogams and Ferns," a task which the author regarded as the extreme of drudgery. The older morphology included more or less of this material, for in those days one fact was just about as important as another, and some of these anatomical facts were conspicuous enough for even elementary students to recognize. As is well known, the newer morphology eliminated this whole enormous body of material. The reason is evident and sufficient. It was so completely unorganized that it could not be used in any phylogenetic structure; and the reproductive structures could be so used. All but the blindest morphologists recognized that this vast accumulation of so-called anatomical material would have to be reckoned with some day. It has now developed that the vascular system has been the first thing organized out of the

anatomical rubbish pile, and it has been promptly and warmly welcomed by modern morphology.

The organization of vascular anatomy upon an evolutionary basis came at a most auspicious time, for the phylogenetic lines, guarded only by the anatomy of reproductive structures, had begun to show signs of wavering. Wider researches had begun to dissipate rigid categories into mists. Such veterans of definition as archesporium, sporangium, sporophyll, etc., had been put to flight. Especially did experimental morphology play havoc. It made hereditary structures lose their rigidity, and raised the question whether the hen that sits on the eggs is not more important than the one that lays them. It certainly intensified the conviction that any structure might arise any number of times. This made schemes of phylogeny essentially paper schemes. They were good illustrations of what the phylogenetic succession might have been, but they could carry no assurance of what the phylogenetic succession actually had been.

This whole situation has been steadied, at least morphologically, by the recent development of vascular anatomy, including as it does the enormously important ancient history of the vascular groups, which was largely denied to the reproductive morphologist. The difference between matching forms and investigating structure is nowhere more clearly illustrated than in the recent development of our knowledge of fossil plants. Morphology, therefore, really has another ally that came in company with vascular anatomy, and that is actual history, which must always be reckoned with.

As a result of this triple alliance, what has been the progress of morphology during the last decade? Our subject necessarily limits us to the vascular plants; but it might be said, in passing, that most important progress has been made in bryophytes and thallophytes as well.

Students of gametophytes and sexual organs, of spore-producing members, of the vascular system, of fossil plants, have been investigating with wonderful energy,

and all with phylogenetic relations in view. This has meant comparison at every step; and as a consequence, there is available to-day a wealth of important information such as we have never possessed before. The process of sifting has gone along with the work of accumulation, so that our facts are sorted, and in shape to use. We may not use all this material, but whatever has been collected with a phylogenetic purpose must be reckoned with. One interesting result from this wealth of material has been the loosening up of all our conceptions of structures. No definitions have stood; and our statements to elementary classes are all with important mental reservations. This substitution of a general situation for a rigid definition is also a substitution of knowledge for terminology, and introduces into our phylogenetic schemes a conception of variation that makes them workable.

So many definite lines of attack have resulted in still more numerous schemes of phylogeny. Each investigator naturally regards his own field of work as phylogenetically the important one, otherwise he would not be working in it. A detailed examination, however, of all the schemes based upon extensive investigation reveals the fact that the differences have to do in the main with subordinate features. Certain large conclusions may be regarded as fairly well established, so far as our present information goes. Some of them I may venture to mention, for they represent fairly well the progress of a decade. Of course the progress of largest importance is the fact that so much trained investigation is being directed along so many convergent lines that meet in the problem of phylogeny. Never was morphology so well equipped as it is now. The large results to be mentioned are those concerning which there is substantial agreement; which means results that must have stood the test of morphology, anatomy and history.

Discredit has been thrown upon the cell-by-cell studies of such structures as the embryo, gametophytes, sex or-

gans, and sporangia; and upon the layer-by-layer studies of growing points. This means that an immense amount of detailed work has been swept into the limbo for facts at present useless. Early developmental studies of a few forms seemed to establish definite sequences in cell-divisions and definite functions for so-called generative layers. This kind of research was its own corrective, for as investigations multiplied, definite sequences and functions disappeared in a maze of variation. The definite thing proved to be not the details of development, but the general organization developed. For example, the important facts in reference to the development of the embryo are no longer thought to be the sequence of the first dozen cell-divisions, but the organization of tissue systems and organs. The leptosporangiate sporangium may develop in a great many different ways, but the general result is a sporangium of some definite type. Particularly futile has proved to be the detailed study of the development of independent gametophytes, for they react remarkably to environment, and can be made to do almost anything. At growing points it was once supposed that each cell was predestined to contribute to one of the generative layers, and dermatogen, periblem, and plerome were traced through a mass of indifferent meristematic tissue. After organization, they can be recognized; but there is nothing definite in the details of their origin.

It is generally conceded that no great group of plants has been derived from any other existing group. For example, the origin of pteridophytes from bryophytes is hardly a debatable question. The study of reproductive structures alone made such a connection seem quite reasonable to the scientific imagination. We had even selected the responsible bryophyte forms, and showed how *Anthoceros* gave rise to the most primitive leafy sporophyte. Now that much other testimony has accumulated, such a connection is too difficult even for a vigorous scientific imagination. Even the staunchest supporter of this connection, and the one who has worked it out in

greatest detail, has acknowledged its improbability. Bryophytes are no longer thought of as having given rise to pteridophytes, but as illustrating here and there the path along which the ancestral pteridophytes may have traveled. Just how we should classify these ancestral pteridophytes makes no difference until we meet them.

The origin of gymnosperms is another conspicuous illustration of the same point of view. Paleobotany has achieved no greater triumph than the discovery of an extinct group of fern-like seed-plants, commonly called pteridosperms, but better called Cycadofilicales. Our knowledge of the group is remarkably complete, so that their connections present no greater difficulties than do those of living groups. Since most of these old seed-plants had been described as paleozoic ferns, it was assumed at first that this was a demonstration that gymnosperms have been derived from ferns. Sober second thought reminded us that ferns as we know them are essentially modern; that the reputed ancient ferns have turned out to be seed-plants; and that the actual ancient ferns, therefore, are unknown. Conceding even that some of the old fern-like plants are ferns, or Primo-filices as they have been called, which is very reasonable, the record of the fern-like seed-plants is just as old. The ferns as we know them, therefore, probably did not give rise to gymnosperms, but they may well illustrate stages in the evolution of gymnosperms.

The case is still clearer in connection with the origin of angiosperms. When the Gnetales were first studied, the logic of the morphology of that day suggested that they had given rise to angiosperms, and so the connection with gymnosperms seemed to be established. Nothing could be more clear than that flower, embryo-sac, and even vascular tissue were well on their way to the angiosperm condition. But then Gnetales have no discoverable history, and angiosperms have, not to speak of other difficulties. As a consequence, those who are most insistent

upon establishing a phylogenetic connection between Gnetales and angiosperms claim only that they are lines of parallel development from a common hypothetical ancestry. It is the use of history as a check that has changed our point of view as to phylogeny more than any single factor; and it is the recent vascular anatomy that has given us a trustworthy history.

The transformation in our conception of the inter-relationships of pteridophytes deserves mention. Ever since alternation of generations was recognized, the ordinary fern, with its seductive prothallium, has been generally thought of as the living pteridophyte nearest the bryophyte level. It is now recognized that the Filicales, as a whole, are more clearly connected with seed-plants than is any other group of pteridophytes, and that we must look elsewhere for the most primitive living type of vascular plants. Whether we find them in some of our club-mosses or in Ophioglossum may be an open question for some, which vascular anatomy and history are in a fair way to decide. In any event, vascular anatomy and history have strikingly confirmed, in a general way, the conclusions of the morphology of reproductive parts.

The change of view as to gymnosperms has perhaps been the most striking change of the last decade, and this has been brought about by remarkably aggressive work in all lines of approach, beginning with the discovery of swimming sperms in the cycads and Ginkgo. Of course, the most sensational discoveries since have been the existence of Cycadofilicales and the remarkable strobilus of the Bennettitales. These discoveries have been supplemented by morphological work in almost every genus, anatomical work in all the important groups, and an unprecedented uncovering of the gymnosperm history. Now we recognize the group as starting with fern-like plants, bearing microsporangia and megasporangia as the ferns do sporangia. From this start a strobilus was worked out, whether primitively monosporangiate or amphisporangiate or both is not clear. One line (cycadophyte)

retained more primitive characters in its sexual reproduction and vascular system; another line (*Cordaitales*), while retaining the more primitive sexual reproduction, developed a more advanced type of vascular system, which has continued in *Ginkgoales* in one direction, and in *Coniferales* in the other, associated in the latter with a more advanced type of sexual reproduction.

This gymnosperm situation may illustrate a fact that is becoming more and more apparent. On the basis of the older reproductive morphology the cycads are more ancient than the conifers; on the basis of history the reverse is true. The cycads are relatively modern, but have persistently retained certain ancient features; yet the logic of the older morphology would have insisted that conifers are derived from cycads. It is a fact, therefore, that primitive features are not necessarily a mark of age, even among closely related groups. The testimony of all features must be considered, and this checked up by history, before any rational conclusion can be drawn.

The most baffling tangle of relationships among gymnosperms at present is that presented by the tribes of *Coniferales*. The perplexity of the situation is due to the fact that as yet morphology, vascular anatomy and history are at variance. Of course, history must determine the actual sequence, and then our contradictory morphology and anatomy can be straightened out. For example, morphologically in *Taxineae* are advanced; in wood structure they are also said to be advanced; but they are also reputed to retain the old mesarch structure, which would indicate that they are primitive. When we know what they are historically, we can determine whether this anatomical feature is primitive because the group is primitive, or because this character of the bundle has lagged behind. Of course, these "mesarch" bundles may not be mesarch in the old sense, and the centripetal wood may be explained away; if so, the group will be advanced in all its characters and will not need the testimony of history.

This fact of "lagging behind" is coming more and more into evidence. I do not mean by this that the lagging structures always advance sooner or later, for they may simply persist as veterans. A conspicuous illustration of it is found in the evolution of the microsporangiate and megasporangiate structures of seed-plants. In the most primitive group of seed-plants known, the Cycadofilicales, the microsporangia are still at the fern level, produced in the same relations and of the same general structure as are the sporangia of ferns; while the megasporangiate structure has become a highly organized ovule, which in some way has replaced the sorus. The relations to the sporophyll are the same, but the structure has become very much changed. There is an enormous hiatus in our knowledge in reference to the heterosporous ancestors of these primitive seed-plants, but during all that development of heterospory to the seed-condition, the microsporangia remained practically stationary. Even among the Mesozoic Bennettitales, the microsporangia are still fern-like synangia, although a highly organized strobilus has been developed; and among modern cycads the same persistent lagging of the microsporangia is evident. All this means that no single character, however primitive, can establish the phylogenetic level of a group. All the testimony must be in, and especially the history, before one can feel any reasonable assurance as to conclusions.

The new conception of the monocotyledons is so clearly a triumph of vascular anatomy that the other phase of morphology is hardly entitled to a share in it. And yet, now that it is evident that the monocotyledons are a specialized offshoot from the primitive dicotyledonous stock, many things in the older morphology become clearer. There are those intergrades, as they may be called, between the monocotyledonous and dicotyledonous condition, which have given so much trouble to the pigeon-hole botanist, who insists that a given seed-plant must be a monocotyledon or a dicotyledon. We recognize now

that these intergrades are what might be expected, and they occur in the general region which, according to the vascular anatomist, gave rise to the monocotyledonous offshoot. It has always interested me to see how convinced we become by our own definitions. We have legislated that the last resort for distinguishing monocotyledons and dicotyledons is the cotyledon character; all other characters have been found to be liable to exception. I submit it to you whether any single character selected in this way as final arbiter could not function equally well as a character of last resort. This business of last-resort characters is nothing less than harking back to an artificial system. It is hardly conceivable in these days that such a character can really exist. It is the totality of characters that must place an organism, a most difficult test to apply, but none the less essential. A conspicuous illustration of this situation is that of *Selaginella*. It is assumed that the last-resort character of a seed-plant is the seed; and yet no definition of a seed can be constructed that will exclude all species of *Selaginella* and include all seed-plants. Then why is not *Selaginella* a seed-plant? Simply because its other characters forbid such an association. There is no conceivable reason, therefore, why a dicotyledon may not be monocotyledonous and still remain a dicotyledon, or *vice versa*. The vascular anatomist tells us that one of the surest marks of a monocotyledon is the amphivasal bundle; and at the same time he points out amphivasal bundles among dicotyledons.

I am pressing this point perhaps unduly, but there is a growing tendency that should be checked. This is to transfer groups on a single character, or to propose phylogenetic connections without weighing or waiting for all the characters involved. It is easy to construct a satisfactory scheme based upon one character; it has thus far proved impossible to construct a satisfactory scheme based upon all the characters we happen to know.

The spirit that animates modern morphology is nowhere more evident than in its effect upon teaching.

When this type of work was introduced into the laboratories of this country, almost any available material was used. This material was studied in great detail, important and trivial things being kept at a dead level. The purpose was to train in observation rather than to develop any picture of the plant kingdom. This detailed study meant the handling of a few types. The pedagogical slogan of those days was a few types thoroughly studied. The few types selected were naturally those most available, and by some irony of fate these most available things turned out to be the most unrepresentative types possible. You are familiar with the old list: Spirogyra, standing for green algae; Marchantia, for liverworts; a leptosporangiate fern, for pteridophytes, and so on. Now all this has been changed. The purpose is to give some conception of the evolution of the plant kingdom, not in detail or in any rigid way, but in general perspective. The threads on which the facts are strung are such as these: the transition from a one-celled to a many-celled body, the evolution of reproductive methods, the origin and differentiation of sex, the acquisition of the land habit, the origin and development of the alternation of generations, the origin of the leafy sporophyte, the evolution of the vascular system, the evolution of the seed, the origin and evolution of the flower. How can "a few types thoroughly studied" illustrate such things or give any such perspective?

This means much illustrative material, carefully selected, and each form used to illustrate some definite and important fact. It is not many types hastily studied, but many types studied carefully for the few points that are really important. The difference between the older view and the recent one, both in teaching and in research, is the difference between an indiscriminate mass of unrelated details obtained from a few representative forms, and a selected mass of related details obtained from a large number of representative forms.

These somewhat miscellaneous statements may serve

to illustrate the point of view that has been developed, which after all is the significant thing in our progress. It would be tedious and unprofitable to enumerate the long list of important new facts that have been discovered. Besides, these new facts are most of them so technical that any brief reference to them would be intelligible only to those who do not need the information. In closing, I may venture to suggest a future development which seems extremely desirable. The general problems upon which we are now engaged must involve the examination of an enormous amount of material before we can feel any confidence in our conclusions. It ought to be possible to associate investigators or laboratories in a general attack upon any problem conceded to be important enough to justify such a united effort. Whenever this has been done in a laboratory possessing several investigators, the result has been striking. We must begin to combine our detached efforts, the guerilla method of attack, and support individual effort by association. The scheme is only a thought, and the details may make it impossible, but I believe that we have reached a point where something of this kind is demanded for definite and substantial progress.

II. THE PROGRESS OF PLANT ANATOMY DURING THE PAST DECADE

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THE fascinating problem of the alternation of generations in the higher plants is responsible for the fact that the attention of morphologists, since Hofmeister, has been turned largely to the spore-producing organs and the gametophytes. This tendency can be counted as entirely fortunate, for the closer affinity of the gametophyte with the presumably ancestral forms and the progressive re-

duced and simplified structure, which it presents in the vascular series, has made it particularly suitable for the initial stages of modern morphological development. With the discovery of zoidogamous fertilization in Cycas, Ginkgo and the lower fossil gymnosperms, the revelation of the remarkable mode of fertilization in the Araucariaceæ, simulated at least in the Podocarpineæ, the uncovering of the phenomenon of breech fertilization in the lower Amentiferæ and the elucidation of other striking phenomena connected with the male gametophyte, we have come to realize that it is the male sexual generation and the sporogenous apparatus, producing it, which carry the highest phylogenetic interest. The origin of the seed from the megasporangium, although beyond question on general morphological grounds, still largely lacks illuminating facts to lighten the darkness of its past.

The more complicated sporophytic generation of the higher plants, except as to its special sporogenous structures, has much more recently been attacked by evolutionary morphologists. Its very complexity, however, and the possibility of following its structures into the remotest past, make it of the greater importance from the standpoint of the theory of descent. The evidence derived from its study serves, moreover, to control, amplify and enrich the conclusions reached from the standpoint of the morphology of the gametophyte alone. We have, accordingly, begun to realize that the anatomical examination of the sporogenic organs of vascular plants is quite as important as the cytological study of the process of sporogony itself, and that the fern-like mode of fertilization obtaining in the lower gymnosperms, living and extinct, has its not less important or significant equivalent in the presence of cryptogamic or centripetal primary wood. In fact, with the realization of the importance of the sporophytic generation in the higher plants, we are now for the first time in a position to begin our phylogenetic book-keeping by double entry, with greatly added security as to the final accuracy of the balance we may strike.

Perhaps nowhere is the advantage of morphological bookkeeping by double entry more clearly illustrated than in the case of the conifers. Forming with the other living gymnospermous species a restricted but illustrious "four hundred," they have quite held their own in botanical interest, in spite of the overwhelming numbers and importance of the modern mob of angiosperms. The older and entirely superficial morphology, led to the conclusion that simple forms and structures are more primitive. On this basis the conclusion was reached that those simple and coneless conifers, the Taxineæ or yews, are the oldest and that the pines or Abietineæ, with their very complicated cone-structures, are most modern. It has, moreover, been inferred that the coniferous tribes represent a series of progression beginning with the yews and ending with the pines. The microscopic study of the gametophytes began the disintegration of this system. The discovery of zoidogamous fertilization in *Ginkgo*, which in Engler and Prantl's *Natürliche Pflanzenfamilien*, you will find included with the yews, made it at once apparent that this remarkable genus, sole survivor of an abundant stock, once flourishing through the entire northern hemisphere, could not be included under the Taxineæ, or link the latter with the still more ancient Cordaitales, confined to the Paleozoic. Thus deprived of the reputation of an illustrious ancestry, the yews have since been disrespectfully kicked up the phylogenetic stairs by the younger generation of gametic morphologists. A corresponding but reversed process has in the meantime taken place at the other end of the coniferous series. It has been shown by the gametophytic morphologists, that the sexual generations of the pine tribe are more complicated, and for that reason more primitive in the reduced members of the alternation, than any other conifers, characteristically found in the northern hemisphere. From the sporophytic side it has been shown that the cone-structure of *Pinus* affords an anatomical explanation of the strobilar organization of the other tribes of conifers on the basis

of commonly accepted principles of reduction and adhesion. Further, it has recently been discovered that the leaves of the ancestral pines (*Prepinus*) had the same cryptogamic type of centripetal wood-bundles, which are found in the Cordaitales, universally regarded as the Paleozoic stock to which the conifers as a whole are most nearly allied. There is further evidence of the antiquity of the Abietineous or pine tribe based on important experimental data and on the origin of coniferous pitting, which need not be entered upon here. If, in accordance with the facts very briefly indicated above, we cast up our phylogenetic balance by double entry for *Pinus*, we find it on both sides overwhelmingly in favor of the superior antiquity of the Abietineæ, or pines, as compared with the Taxineæ, or yews. It would take much too long to cast even hastily the balances for the remaining tribes of conifers and in the case of those at present mainly or wholly confined to the southern hemisphere the data are as yet not complete. Even though the books are not yet ready to be opened for the final judgment, the results of recent morphology on both the gametic and sporophytic sides make it clear that the conifers, contrary to the conclusions of the old superficial morphology, are a series of reduction and not one of progression and that their most complicated forms are consequently the oldest and those of simplest guise the most modern.

One of the most striking confirmations of the truth of the theory of organic evolution is found in the recapitulatory phenomena of animals. The colt, for example, in the course of its individual development passes through the phases of progressive loss of digits, presented geologically by the equine stock from the Mesozoic to the present. The young mammal in its earlier stages of ontogeny possesses the gill arches and the segmented musculature of the fish. In the principle of recapitulation presented so clearly in the development of animals, our zoological brethren may fairly claim that on their side of the house the truth of evolution is declared by the

months of babes and sucklings. Although our seedlings, unlike the sucklings, are dumb, they are by no means speechless. One of the most striking triumphs of modern plant anatomy is to have discovered many examples of recapitulatory confirmation of the principle of evolution. To take a modern and striking instance, let us consider our common and flourishing northern genus, the oak. You are all familiar with the very broad rays which constitute so ornamental a feature of the structure of oak wood. You are likewise doubtless aware that the weight of paleobotanical evidence speaks for the derivation of the oaks from ancestors resembling the chestnuts since the older oaks approach the chestnuts both in their foliage and in their reproductive organs. The wood of the chestnut differs, however, strikingly from that of oaks by the entire absence of large rays. It has been recently discovered that certain oaks of the gold-gravels (Miocene Tertiary) of California have their large rays composed of aggregations of smaller rays. In the seedlings of certain of our existing American oaks this condition, interestingly enough, is a passing phase, which by the loss of the separating fibers in the congeries of small rays produces the characteristic large rays of the adult. This condition of development in the living oaks is all the more significant because in certain breech-fertilized or chalazogamic amentiferous trees of the present epoch, such as the alder, the hazel and the hornbeam, such aggregated so called false rays are a permanent feature of structure in the adult. From the anatomical side, in the case of the lower Amentiferae, we have accordingly at the same time an interesting example of the general biological law of recapitulation and a confirmation of the view expressed by Treub and Nawaschin, on evidence from the gametophytic and reproductive side, that the breech-fertilized Amentiferae are relatively primitive angiosperms.

Perhaps the most valuable service which anatomy is rendering to phylogeny and evolution is in connection

with the elucidation of the affinities of extinct plants. Certain cryptogamic trees of the Paleozoic, the Lepidodendrids, Sigillarians and Calamites, were, for example, long regarded by competent botanists as seed plants on account of their arboreal habit. The anatomists stoutly maintained, however, that from the structure of their primary wood they must be cryptogams. The subsequent discovery of their reproductive structures entirely confirmed the anatomical view. More recently from the study of the anatomy of certain fern-like plants with secondary growth, from the Paleozoic, English and German anatomists reached the conclusion that they were gymnosperms and allied at once to the ferns and to the cycads. Within the past decade, the brilliant discoveries of Oliver, Scott, Kidston, Grand'Eury and David White in regard to the nature of the reproductive organs of these plants, prophetically dubbed by Potonié, the Cycadofilices, have confirmed the truth of the anatomical view as to their affinities in every particular. Let us take a still more modern instance. There are present in the later Mesozoic strata huge quantities of impressions of the cones and leafy twigs of conifers. These have been referred on features of superficial resemblance to a number of genera of living conifers as well as to others not represented in the existing flora. Since they are very numerous, let us take one typical example, which is at the same time significant. Many species of *Sequoia* have been described from the upper Jurassic and the Cretaceous beds, on the evidence of the impress upon the stony or argillaceous matrix of their cones and leafy branches. Dr. Arthur Hollick and the present speaker have been fortunate enough to secure by new methods of isolation, material of these cones and twigs, with internal structure preserved. The anatomical features of both reproductive and vegetative organs of the remains in question, show beyond any possible doubt that they belong to a tribe of conifers at present confined to the southern hemisphere, the Norfolk Island and Kauri Pines

or Araucarineæ, and have not even the slightest affinity with the living genus, which externally they so strikingly simulate. The reference of the fossil genus just described to its true affinities as well as similar results in the case of a large number of other Mesozoic conifers, likewise erroneously placed in the system, leads to important general conclusions in regard to the evolutionary history of coniferous gymnosperms, which are too lengthy and too technical even to be mentioned here.

But it is not only in connection with extinct plants that anatomy has shown itself the useful servant of phylogeny. The enforced use of anatomical criteria in the case of fossil forms, where such evidence is absolutely indispensable, has resulted in a new and broader point of view in general botanical morphology. Within the decade we have begun to realize fully the great constancy of fibro-vascular structures. This may perhaps be best exemplified by a special case. Superficially there is no organ of the plant more prone to vary extremely, within near lines of affinity, than the leaf. If, however, we look within, it presents anatomical features of great constancy. In the case of the leaf, perhaps the most hopelessly variable feature is its size. Anatomically, however, there are just two sizes of leaves, large leaves (megaphylls) and small leaves (microphylls), which are absolutely characterized by their anatomical relations. The foliar strands of the megaphyll, or large leaf, pass off from the woody cylinder of the stem, leaving corresponding gaps in its wall. Those of the microphyll, or small leaf, equally constantly leave no such gaps in their exit from the woody cylinder. It is even possible to divide the whole vascular series into two clean-cut phyla on the basis of the anatomical features of leaf size, viz., the Pteropsida with, anatomically speaking, large leaves, including the ferns, gymnosperms and angiosperms and the Lycopsida, structurally speaking, small leaved forms including among living plants only the club-mosses and horsetails.

I have tried to show above, with all necessary brevity, that the services of anatomy to phylogeny and the doctrine of descent during the past decade have been neither few nor unimportant. Perhaps the most important general result of recent work in the modern morphological field, not restricting it, of course, to anatomy, may best be expressed in the words of the eloquent and philosophical apostle to the gentiles, viz., that the things seen are temporal, while the things unseen are eternal. You may think that I have too much emphasized the importance of internal morphology. One example will serve to show that I have not. You are all familiar with that great German work on the morphology (or, as its author prefers to call it, the organography) of the higher plants, which not very long ago appeared in a *traduction de luxe* from the Oxford University Press. If you scan it from cover to cover, I do not believe you will find a single figure of the fibro-vascular structures. Not even the proverbial halfpenny's worth of bread is present to qualify the oceans of sack. It is not surprising that we should hear from such a source a strong note of morphological pessimism. On a recent occasion in our own country, the distinguished author of the work in question compared the task of his science to that of Sisyphus, of classic fable, condemned to roll up the mountainside a stone which continually rebounds. We may confidently expect that the morphology of the future, distrusting the superficial anfractuosities of the steep, will bring the profitless rolling stone to rest in the very heart of the mountain itself.

SHORTER ARTICLES AND CORRESPONDENCE

A NOTE ON THE DEGREE OF ACCURACY OF BIOMETRIC CONSTANTS

The statement is frequently made, either in comment or criticism upon biometric work, that such work is often caused to take on an unwarranted appearance of precision and exactness by the keeping of a larger number of decimal places in the tabled constants than the character of the original data justifies. The contention is made that under no circumstances whatsoever can any statistical constant be more accurate than the data on which it is based. It is held that if one makes a series of measurements accurate to a tenth of a millimeter, it is a logical absurdity to table the mean or standard deviation deduced from these measurements to hundredths of a millimeter. Not only is this contention made from time to time by biologists, but occasionally even by a mathematician, a fact which of course tends strongly to confirm the biologist in his opinion. Thus Engberg¹ specifically says (p. 11) referring to mortality statistics: "The constants can not be more accurate than the data on which they are based."²

The reply which the statistician makes to the criticism that constants can not be more accurate than the data on which they are based is generally that the accuracy of a statistical constant depends not alone on the accuracy of the original measurements but also upon the number of such measurements. Further it is pointed out that, because of this fact, it is possible to deduce from measurements known to be individually inaccurate constants of a high degree of accuracy, *provided* that the errors in the measurements are unbiased (that is as often in excess as in defect of the true value) and that there are enough of the data. Finally the statistician contends that the only proper measure of the accuracy of a statistical constant

¹ Engberg, C. C. The Degree of Accuracy of Statistical Data. *Univ. of Nebraska Studies*, Vol. III, No. 2, pp. 1-14, 1903.

² In passing it may be said that any one who is sufficiently interested in the phenomenon of a professional mathematician taking this curious position will find an entirely adequate and satisfactory discussion of the matter in *Nature*. Vol. 69, p. 93, where Engberg's paper is reviewed.

(always assuming that the original data are not collected in a deliberately dishonest or biased manner) is its "probable error." Unfortunately this statement of the case appears not to carry conviction to the non-statistical worker. It has seemed to the writer that if the assertion made by the statistician regarding the point under discussion is true, it ought to be possible to demonstrate it in such a manner as to carry conviction to anybody.

With this object in view the experiment to be described was tried. Some time ago the writer measured for another purpose the lengths of 450 hens' eggs. The measurements were made with a large steel micrometer caliper manufactured by Browne-Sharpe & Co., reading directly to hundredths of a millimeter. The utmost care was exercised in the making of the measurements; they were all made under the same conditions as to light, temperature, etc.; the caliper was held in a specially constructed stand to get rid of the error arising from expansion and contraction if it is held in the hand; the micrometer screwhead was fitted with a ratchet which mechanically insures that the same pressure shall be exerted on the object in every case; all measurements were made by the same observer who has had considerable experience in close micrometer measuring. The maximum length was the thing measured. There is every reason to believe that these measurements to hundredths of a millimeter are as accurate as it is possible to make them with the instrument used. This being the case all will agree that any statistical constant deduced from them can be held to be accurate to hundredths of a millimeter at least. Now let it be supposed that these eggs had been measured only to the nearest millimeter instead of to the nearest hundredth of a millimeter. By how much would the statistical constants deduced from the "millimeter" data differ from those deduced from the "hundredth millimeter data?"⁸

To answer this question it is necessary to calculate some statistical constant for the two sets of data. The mean was chosen as the simplest possible constant. The actual measurements to hundredths of a millimeter were used as one set of data. The "millimeter" data were obtained by discarding the decimals of the original measurements. In this discarding a record was raised 1 mm. whenever the decimal portion of the original

⁸The biometrician will, of course, recognize that the problem here involved is the same as that of the influence of the fineness of grouping on the value of constants.

figure was .51 or greater. When the decimal part of the record was .49 or less the integral part stood unchanged. In the 450 measurements there were six cases in which the decimal portion of the record was exactly .50. In one half of these cases the record was raised 1 mm. and in the other half was left unchanged, when the decimals were discarded. This is obviously the only fair way of dealing with such cases since, for example, 51.50 is exactly as near to 51 as it is to 52.

The original measurements and the "millimeter" data after discarding the decimals were then each added and re-added with a calculating machine. The resulting sums were:

When the measurements were kept to the nearest hundredth of a mm. When the measurements were kept to the nearest whole mm.

Dividing each of these figures by the total number of cases, 450, we get for the means the following:

Mean from " hundredth mm. data " Mean from " millimeter data "
 56.315 56.324

The difference between these two figures is .009. That is, there is no difference between the two averages until the third decimal place is reached. To two places of figures both means are 56.32. But this can only mean that the mean or average obtained when the records are made only to the nearest millimeter is *more* accurate, by two places of decimals, than the data on which it is based.

In interpreting this statement of fact it must not be held to signify that biometric measurements should not be made with the greatest attainable degree of accuracy. Because statistical constants, when the number of cases dealt with is large, are more accurate than the data on which they are based gives no excuse for rough measuring. The reason for this, of course, lies in the principle, which actual experience shows to be correct, that the finer and more accurate the measuring the less chance of the data being unconsciously biased. Statistical constants can only be more accurate than the original data when the data are strictly unbiased. The "applied psychology" of practical measuring teaches that unconscious bias goes out of the records just in proportion as the measurements are made finer.

RAYMOND PEARL

MAINE EXPERIMENT STATION.

PURE STRAINS AS ARTIFACTS OF BREEDING

Students of the minute anatomy of plant or animal tissues are on their guard against artifacts. Chemical reagents often contract or coagulate the protoplasm or cause the precipitation of granules or crystals. The artificial results of the methods of preparation have to be distinguished from the normal structures of the protoplasm. Precautions are equally necessary in the study of evolution and heredity, to avoid mistaking artificial products of breeding for typical conditions.

Close-bred, uniform groups of plants and animals form the basis of the idea of "pure strains," "elementary species" or "biotypes." If the descendants of the same parents appear sufficiently alike the strains are said to be "pure." General inferences regarding heredity and evolution are being based on the assumption that this uniform "purity" represents a natural condition. Yet there can be no doubt that the methods used in maintaining and testing the purity of strains are calculated to produce an artificial uniformity of characters, commonly accepted as the proof of purity.

If the habits of a plant will permit, the readiest method of securing uniform progeny is by vegetative propagation. Nevertheless, the idea of pure strains is not usually connected with vegetative varieties, for it is recognized that uniformity lasts only while vegetative propagation is continued. As soon as seeds and seedlings are grown the natural individual diversity reappears. The vegetative propagation only conceals the inherent diversity by devices that avoid the production of seedlings.

The uniformity of groups of seedling plants is of the same artificial nature as the uniformity of vegetative varieties. Particular methods of reproduction are necessary to secure uniform seedlings—methods which may not be essentially different from those represented by cuttings or offshoots. Plants grown from buds or cuttings have only one parent, and the same is true of seedlings produced by self-fertilization. It is only when conjugation is restricted to cells of the same individual or of closely related individuals that uniform seedlings are obtained. The external formalities of conjugation are preserved, but without the essential diversity of descent which gives conjugation a physiological significance.

The uniformity of varieties of wheat and other strictly self-fertilized plants depends as closely upon self-fertilization as

the uniformity of vegetative strains upon vegetative propagation. As soon as individual wheat plants are crossed, even inside the same variety, a wide range of diversity reappears. Self-fertilization, like vegetative propagation, brings uniformity by suppressing the inherent tendencies to diversity. Pure strains continue to seem pure as long as only one set of characters is brought into expression, but the latent diversities do not cease to be transmitted, and at once reappear when hybrids are made, or selection is relaxed, or the plants are transferred to new conditions.

It is true that uniformity like that of the pure strains of domesticated varieties is sometimes found in nature, but even this does not prove that uniformity represents a truly normal condition of reproduction. Having learned that artificially restricted descent produces uniformity in domesticated varieties, it is easy to understand that natural conditions of close breeding can also produce uniformity.

The methods of reproduction that yield uniform offspring often appear very effective from the environmental standpoint, but this only shows the more plainly their physiological inferiority. All indications point to the probability that long-continued vegetative propagation, self-fertilization or close breeding bring the same deterioration, sterility and ultimate extinction to wild types as to domesticated varieties. It does not appear that the vigor and fertility of organisms can be permanently maintained by the methods of reproduction required for pure strains. Free interbreeding among diverse individuals to form a continuous network of descent is the natural relation of the members of species.

The physiological inferiority of pure strains forbids our acceptance of theories of evolution and heredity based upon the idea of uniformity. Neither uniformity itself nor the attendant phenomena of mutation and Mendelism represent primary biological facts, typical of organic existence and evolutionary progress. The restriction of descent to closely similar and closely related individuals is a change from a natural state to a relatively artificial, atypical condition. Darwin saw in the facts of Mendelian inheritance a definite evidence of the abnormality of mutations, but the significance of this relation is not fully appreciated until we perceive that the uniformity of pure strains already marks a first step toward degeneration.

WASHINGTON, D. C.,
February 10, 1909.

O. F. COOK.

NOTES AND LITERATURE

HEREDITY

The Nature of "Unit" Characters.—One of the clearest presentations of Mendelian principles that has appeared recently is that of Dr. E. Baur in *Beihefte zur Medizinischen Klinik*, Vol. 4, 1908, pp. 266 et seq. He has given special attention to inheritance in crosses between the various varieties of *Antirrhinum majus*. He states that he knows 250 distinguishable varieties of this species, but he has never found amongst them characters that do not obey Mendel's law. He has demonstrated fifteen pairs of characters for the species, which is more than the number of chromosomes present, from which fact he concludes that the chromosome as a whole can not be considered as the basis of Mendelian unit characters. Others have cited as a basis for the same belief that more character pairs are known in *Pisum* than there are chromosomes present in the cells. This conclusion is not a necessary one, as is seen in the following. Speaking in a general way, the chromosomes are present in pairs of homologues. For each pair in the cells of a given individual there is a homologous pair in the cells of other individuals of the species. For convenience we may designate one of these pairs as A chromosomes, a second as B chromosomes, etc., the same pairs as a rule being found in different individuals of the same species.

If we consider the species as a whole, the number of pairs of A chromosomes is equal to the whole number of cells in all the individuals of the species. It is conceivable that, since certain of these A chromosomes may trace back thousands of generations before their ancestral lines unite, it is possible that there may be an indefinite number of subgroups of A chromosomes in the species, and that each subgroup may represent a heritable difference from other groups. But each of these subgroups would represent a Mendelian character. Hence, there might possibly be an indefinite number of Mendelian character pairs in a species having only a single pair of chromosomes.

But these characters could not all exist in one individual. Only two of the subgroups could be present together. Hence, in such a species, only two independent (not correlated) domi-

nant characters could be present, and these two would present a case of what Bateson calls spurious allelomorphism, for they would separate from each other in the reduction division.

It is clear, therefore, that the presence *in a species* of more Mendelian character pairs (presence and absence constituting a pair) than there are chromosomes does not prove that Mendelian characters do not appertain to the chromosome as a whole. If, however, in a species having one pair of chromosomes we could get *into a single individual* more independent character pairs than two, or if we can get even two dominant characters that are independent of each other, and not allelomorphic to each other, then we should have proven that Mendelian characters do not appertain to whole chromosomes. In general, if, in a species having $2n$ chromosomes, we can bring together in a single individual more than n independent dominant characters, no two of which are allelomorphic to each other, then it would be proved that Mendelian phenomena are not simply phenomena of the chromosomes. In a recent communication to the writer, Dr. Baur recognizes the justice of the above point of view and hopes to be able to test the matter in the near future. Dr. Shull will make a similar test at the Cold Spring Harbor Station. This, it would seem, is a simple and direct method of testing the validity of the theory advanced by many investigators, that the chromosome itself is the basis of the so-called unit character.

Even if this theory should be substantiated, it does not follow that the chromosome represents a unit character in the sense in which the term unit character is understood by most Mendelists. Shull has very justly pointed out¹ that "there is no evidence of the existence of a pair of internal units (allelomorphs)." The term "unit" has been applied to Mendelian characters on the assumption, which I regard as untenable, that there is in the germ plasma a definite organ set aside for each hereditary character. An elaborate theory of inheritance and evolution (De Vries) has been erected on this assumption. Mendelian phenomena can be explained in a wholly different manner, and one which is more consistent with the idea of the chemical basis of life processes, as the following illustration shows.

Let us designate the chromosome pairs in our common domesticated cattle as A, B, C, . . . L. Let us assume that the chromosomes in each of these pairs are capable of several types of metabolic activity, and that each of them, by its action on the nutritive materials furnished it, gives rise in the cell to as many

¹ See *Science*, February 12, 1909.

metabolic products as it has metabolic activities. Doubtless some of these products will be similar for a number of chromosomes. We may thus represent the chromosomes and their functions:

(AA) — functions a, b, c, d,
(BB) — " b, c, d, e.
(CC) — " a, b, d.
(EE) — " a, b, f.
Etc. Etc.

Now, of the numerous B chromosomes in the species, some may perform the function e in a manner differing from the others. This function may fail entirely in some of them. Let us assume that the production of horny substance requires that the functions a, b, e and f shall be normal. If in a given group of individuals the function e fails, which function may represent the production of a given chemical substance in the cell, then horns fail to develop. Individuals without horns would thus be represented as follows:

(AA) — a, b, e, d.
(BB) — b, e, d.
(CC) — a, b, d.
(EE) — a, b, f.
Etc. Etc.

Omitting from consideration those chromosomes which are not concerned in the hereditary difference in question and remembering that the poll character is dominant, the heterozygote between the horned and polled forms would be

B — b, e, d, e; B — b, e, d (heterozygote polled).

Generation F₂ would consist of

1. B — b, e, d, e; B — b, e, d, e (horned).
2. B — b, e, d, e; B — b, e, d (heterozygote polled).
3. B — b, e, d; B — b, e, d (homozygote polled).

or three polled to one horned. Thus we derive the well-known Mendelian ratio entirely independently of any idea of unit character in the germ plasm. Rather we assume that horns are due to the presence in the cell of certain substances each produced by the chromosomes, as a result of their *chemical constitution*; and the poll character is due to the failure of a *single* chromosome to perform a particular function. When a hereditary difference between two varieties is thus due to a difference in a *single* set of homologous chromosomes, such difference will be-

have as a simple Mendelian character. If it be due to differences in two sets, it will behave as a compound character of two factors, and so on.

All known Mendelian phenomena may thus be explained as due to differences in the chemical constitution of the chromosomes in different groups. It is thus seen that Mendelian phenomena lend no support to the theory that each hereditary character is represented in the germ plasm by a separate entity.

The question as to the nature of the chromosome differences which are thus seen to be able to account for the phenomena first interpreted by Mendel will be considered at another time. The differences between the metabolic activities of homologous chromosomes here assumed may be due to differences in the relative amounts of given substances in the chromosomes concerned, or they may be due to differences existing in different regions of the chromosomes. In the present state of our knowledge of the chromosomes we are not ready for any theory on this point. Should Shull or Baur succeed in getting into a single individual more independent (neither correlated nor allelomorphic) dominant characters than there are chromosome pairs, then we shall at least know that the chromosome as an individual structure is not responsible for Mendelian characters. This is the one question which must be settled before Mendelian theory can make further progress.

Much recent work has been done which bears on the relation between chromosomes and hereditary characters.

First of these should be mentioned the important contribution made by Professor E. B. Wilson, published in *Science*, January 8, 1909. This paper is so accessible that it is unnecessary here to review it in full. Suffice it to say that Professor Wilson and his students have demonstrated an important relation between sex and certain chromosomes and chromosome groups. In general, the cells of the species studied contain an "X-element" which in some species consists of one chromosome, in others of two, in others three, and in one species of four chromosomes, but which acts as a unit in the reduction division; *i. e.*, all the chromosomes of the "element" pass to the same pole. In all the species studied, the cells of the female contain two of these X-elements, while those of the male contain but one. The males of some of the species contain no homolog (synaptic mate) for this element, but others contain an element which Wilson calls the Y-element, with which the X-element pairs in the reduction division. In every case the Y-element, when present, consists of a

single chromosome. In every case, therefore, the female is homozygote for the X-element, while the male is heterozygote either for X and Y, or for X and absence of X. Wilson shows that the above relations hold in a wide range of organisms, and suggests that it may be a very general relation. There are reasons however, for suspecting that the relation is not the same for all organisms. In a previous paper² I pointed out a number of cases which indicate that the female may be heterozygote and the male homozygote for sex, though some of the phenomena cited may be explained on a different basis. Miss Durham and Miss Marryatt³ have recently worked out one of the cases referred to in my former article, which is a case in point. In certain strains of canaries, black-eyed females mated with red-eyed males give only black-eyed males and red-eyed females. This may be explained, as the authors point out, by assuming a correlation between eye color and sex. Letting X represent the chromosome element characteristic of the female and Y that of the male, assuming that Y is responsible for black pigment in the eye and that in some individuals Y has lost the pigment-producing power, the facts are rendered intelligible by the following assumptions regarding the gametic constitution of the types:

Black-eyed female = X Y-B, in which Y and B belong to the same chromosome element.

Red-eyed male = Y-b Y-b, where the function B is absent.

Here the females produce two kinds of eggs, namely, X and Y-B, while the males produce one kind of sperm (Y-b). This gives progeny of two types, namely, X Y-b (red-eyed females) and Y-B Y-b, black-eyed males. All the phenomena cited by Miss Durham and Miss Marryatt are explicable by assumptions similar to the above, though the occasional occurrence of black-eyed hens in the mating of black-eyed hens with pink-eyed cocks renders it necessary to assume that in some hens the X-element can also give rise to black pigment, or at least stimulate its production in some other element.⁴ The facts cited in my previous paper regarding the inheritance of the bar character in the plumage of poultry further indicate that the female and not the male may be heterozygote for sex, as do also Doneaster's results

² AMERICAN NATURALIST, September, 1908.

³ Rep. IV, Evol. Com., Roy. Soc.

⁴ The gametic constitution here assumed is not that of the authors. They assume that B and Y are separate, but that B is "repelled" by X, thus giving the same results as above.

with the moth *Abraxas*. It is hoped Professor Wilson may be able to make cytological studies on some of these cases.

The fact that such characters as eye color in canaries, barring in poultry, and melanic types in *Abraxas* may be coupled with sex points strongly to the chromosomal nature of these characters. The work of Professor R. R. Gates, and that of Miss Annie E. Lutz on the chromosomes of *Oenothera* points strongly to the assumption that chromosomes are the elements with which we have to deal in the study of hereditary characters. Their results indicate that mutations of the De Vriesian type are due to accidents in mitosis. Miss Lutz remarks:⁵

The numbers of chromosomes are closely associated with external characters in the first and last, and probably also in the second group.

Professor Gates has also expressed the opinion that abnormal chromosome behavior may account for the mutation phenomena observed by De Vries. It seems probable, therefore, that mutations of this character do not represent what we may call normal evolutionary changes, but that the latter must be sought in changes in the chemical constitution of the chromosomes.

W. J. SPILLMAN.

ENVIRONMENT

The Effect of Environment upon Animals.—"Katy-did, Katy-didn't" seems to continue to be a fair summary of the situation with respect to the heredity of acquired characters and the part played by environment in evolution. Wallace wrote in the *Fortnightly Review* (January, 1908) restating his belief in natural selection and recommending a careful study of Reid's "The Principles of Heredity" and Ball's "Are the Effects of Use and Disuse Inherited?" Rev. Henslow followed his advice and has published a short, suggestive and very readable book⁴ on "The Heredity of Acquired Characters in Plants," in which he states with even more assurance than before the conclusion of his "Origin of Plant Structures," that "the Origin of Species is due to the joint action alone of the two great factors of evolution—Variability and Environment—without the aid of natural selection." This additional assurance seems to be the result of the growth of the ecological school of botanists and his belief that ecologists are "all at one" in accepting the fact that evolution in plants is the result of the effects of the environment which *can* become heredity.

⁴ *Science*, February 12, 1909.

⁵ London, John Murray, 1908, 107 pp.

In 1876 Darwin had become a true ecologist. In this year he wrote to Professor Moritz Wagner as follows: "The greatest mistake I made was, I now think, I did not attach sufficient weight to the direct influence of food, climate, etc., quite independently of natural selection. When I wrote my book and for some years later, I could not find a good proof of the direct action [*i. e.*, in producing definite variations] of the environment on the species. Such proofs are now plentiful [Henslow says 'universal']."

Plant ecologists . . . are accepting "Adaptation" by response as a *proved fact*. . . . A complete change of front has taken place within the last twenty years, but as Darwin himself was the first [?] to proclaim this view, I called it "The True Darwinism."

Zoologists have been rather behind the botanists in ecological work, but the zoological school of ecology is growing and it does seem true that the more organisms are studied with regard to their relations to their environment, "at home," the stronger becomes the belief in the importance of environment in evolution. Whether this is "True Darwinism" or something else is immaterial, only so it be true.

The most serious difficulty has been to get a good way of accounting for the inheritance of characters produced by the environment. Cunningham² seems now convinced that this difficulty is removed by "hormones," or internal secretions, retracting his former idea that the nexus between secondary sexual characters and the gonads is nervous. Starling's proof that the growth of mammary glands in an unimpregnated rabbit is caused by injection of extracts of fœtuses from pregnant rabbits is given as an illustration of the working of hormones. Applied to the development in phylogeny of horns, for example, it is supposed to work about as follows:

Since the development of the somatic sex-characters is due to the stimulation of the cells by a hormone derived from the gonad, it is conceivable that the gametes may be affected by the internal secretion of the somatic cells whose development constitutes the sex-character. It is quite possible that the hormone in the case of the gonad, perhaps in all cases, is merely the waste product of metabolism occurring in the cell-multiplication. Whether this is so or not, the somatic sexual structure, such as the antler, would naturally excrete into the blood special substances, and these being in the blood the gametes would be multiplied and developed under their influence. We can not suppose that all cells or parts of the body produce living gemmules which are collected in the germ-cells, but we have reason to conclude that all

²"The Heredity of Secondary Sexual Characters in Relation to Hormones, a Theory of the Heredity of Somatogenic Characters." *Archiv Entwicklungsmechanik*, XXVI, 3, 1908.

parts of the soma give out to the blood specific chemical substances which have a marked effect on development, and in presence of which the gametes develop. If we suppose that certain parts, *e. g.*, the frontal periosteum in the ancestors of deer, are stimulated to hypertrophy by external stimulation, this entails an increase in the hormone produced by this part of the body, and this hormone will affect the protoplasm of the gametes which obtain their nourishment from the blood. Mendelians and the majority of modern authorities on heredity and evolution assume that certain material parts of the gametes correspond and determine particular parts and characters of the soma, and therefore the hormones derived from these parts of the soma may well have an influence on the corresponding determinants in the gametes. . . . I must of course assume different hormones for different bones of the body, so that increased hormone from the frontal bone causes modification of the determinant corresponding to that bone, not of bone in general. Thus we have a material chain of influence from a particular part of the soma to the gamete, and from the latter to the corresponding part in the next generation. Whether this suggestion be true or not, it at least destroys the contention that we can not form a conception of the means by which a change in the soma can effect a corresponding part in the descendant. The hypothesis I have suggested would explain ordinary adaptations more easily than secondary sexual characters. It might be applied, for instance, to the hoofs, toes and legs of Ungulata. I hope soon to test my hypothesis by physiological experiment. If there is an influence from the parts of the soma to the determinants of gametes, then an ovary of one kind of animal grafted into another, ought to show an alteration in the character of the individuals developed from that ovary.

The author has apparently not seen an account of Guthrie's work of grafting ovaries. However, it is far from certain, or believable, that specific hormones are given off when the head is rubbed, which affect specific determinants in the germ which cause that specific part of the head to hypertrophy in the next generation in the special sex corresponding to the germ whose containing soma had its head rubbed. Doubtless there are those who would consider this to be complicated pangenesis worse complicated. There seems to be a further point consistently ignored by adherents to such a theory. They point out that only those animals have horns which fight by butting and believe that this proves that horns are developed by butting. They imply that if horses fought by butting they would develop horns; but it seems rather likely, on the other hand, that if horses had horns they would fight by butting. Cunningham, himself, quotes Rörig to the effect that stags with no antlers guard the females,

not by butting, but by fighting with their fore feet. Likewise Henslow claims that similar structures in widely different plants in similar environments prove that these structures were directly produced by the environment. On the other hand, it can not be denied that some of these cases may be due to the similar selective action of similar environments.

Even Weismann was prepared to admit the inheritance of acquired characters in Protozoa, but Jennings⁴ has thrown experimental doubt upon that also. In a second paper⁵ he shows that the environment is, indeed, a large factor in determining the size of *Paramecium*, but, as yet, he has found no proof that these effects are inherited. Even selection seems powerless to affect the size within a "pure line." However, pure lines differing in size can easily be isolated by selection, thus confirming by a zoological example the results reached by several botanists, notably Johannsen. The variation curve of size is considered to be formed by a mixture of pure lines whose dimensions are modified by the environment and growth factors.

FRANK E. LUTZ.

EXPERIMENTAL ZOOLOGY

Hybridology and Gynandromorphism.—Raepke¹ has made a detailed examination of some of the hybrids (bastards) between certain species and varieties of *Smerinthus* (*ocellata*, *populi* and its variety *Austanti*). The material was obtained from the famous hybridologist Standfuss.

The anatomical results may be summed up as follows:

The internal genitalia of the normal male moths show much variation but in the hybrids the variations are more extreme; and often amount to "anomalies," and monstrosities, in the internal organs. Sperm elements are present and reach different stages of maturity, most of them degenerate later, producing a few imperfect spermatozoa. The female hybrids show also greatly modified sexual anomalies, both the germinal region as well as the ducts may be abnormal or even absent. Hand in

¹"Heredity, Variation and Evolution in Protozoa. I. The Fate of New Structural Characters in Paramecium, with Special Reference to the Question of the Inheritance of Acquired Characters in Protozoa." *Journ. Exp. Zool.*, 5, pp. 577-632, 1908.

²"Heredity, Variation and Evolution in Protozoa. II. Heredity and Variation of Size and Form in Paramecium, with Studies of Growth, Environmental Action and Selection." *Proc. American Phil. Soc.*, XLVII, 190, 1908.

³Raepke, W. *Jena. Zeitsch. f. Naturwissens.*, XLIV, 1908.

hand with these modifications there appear male secondary sexual characters in the female as more or less rudimentary male genital appendages at the end of the body. It would seem to follow that the female is heterozygous, a fact of some general interest. The discovery raises once more the question of the cause of gynandromorphism in insects, for obviously these hybrid moths show adumbrations at least of such a condition. In this connection it is of interest to give Raepke's summary of Standfuss's results regarding the sex of hybrid moths and the occurrence amongst them of gynandromorphism.

He classifies the results under five headings:

First, those hybrids that are so abnormal (atypic or sexless) that their sex can not be determined.

Second, those hybrids in which only one sex develops, generally the male; females also rarely appear, but these so imperfect that reproduction is impossible. The males also are sterile.

Third, those hybrids in which both sexes appear in normal proportions; the females sterile, the males crossed back to the parent species fertile in various degrees. The offspring of such a union are, however, very abnormal and monstrous both in their primary and in their secondary sexual organs. *In certain series gynandromorphs appear in surprisingly large numbers.*

Fourth, those hybrids in which the females although appearing normal lay either no eggs or abnormal eggs. The males are like those in the last category or like those in the next.

Fifth, those hybrids in which the females produce fertile eggs. These eggs produce only embryos or if the caterpillar stage is reached at all the young are weak. Whenever it has been possible to rear moths by crossing back these females to the parent species (or from the male hybrids of the same cross) only males develop but in such scanty numbers that they have not been tested further.

Whether in the last instance only males are produced because they are hardier than the females or because of some more fundamental relation is not evident from the results.

On the other hand the italicized statement in the third category calls for further examination. What is the cause of the production of so many gynandromorphs?

Two hypotheses have been suggested in recent years along cytological lines that offer at least a formal solution of the problem. Boveri suggested that the entering sperm fuses not with the female pronucleus, but with one of the nuclei derived

from the first division of that pronucleus. Morgan suggested that the result could equally well be "explained" on the assumption of polyspermy—one sperm nucleus fusing with the egg nucleus and the other (or others) producing cells independently of the segmentation nucleus. The gynandromorphs described by Toyama seemed to be a test case. An analysis of his results gave evidence in favor of my suggestion. In connection with the occurrence of two kinds of spermatozoa in moths—"male and female producing"—the question arises whether on my view the male parts of the gynandromorph are due to a male or to a female producing sperm. In my paper I suggested that since the female sperm is the homologue (from the chromosomal point of view) of the egg nucleus minus its two polar bodies that such a "female-producing" sperm might produce the male parts. This suggestion fits in completely with the view of sex-determination recently adopted by Wilson. It sounds paradoxical at first that a "female-producing" sperm could produce a male soma, yet if we look to the chromosomes alone as sex producers such a view is tenable. Moreover if in the bee there is produced only female-producing sperm—as the evidence strongly indicates—then on my view the male parts must come from a female-producing sperm. On Boveri's view the nucleus that makes the male parts is the same (after one division) as the egg-pronucleus which is also male producing and the homologue of the "female-producing" sperm.

T. H. MORGAN.

ECHINODERMATA

Red Sea Crinoids.¹—Mr. Herbert C. Chadwick has just published the first account of the crinoid fauna of the Red Sea, his paper being based upon a collection made by Mr. Cyril Crossland, under the direction of Professor W. A. Herdman, of the University of Liverpool. From time to time notices have appeared relating to various Red Sea comatulids, but they have been widely scattered, and some of them more or less forgotten, so that before the appearance of this paper an idea of the Red Sea crinoids could only be obtained by a most laborious search through a large number of more or less rare and inaccessible volumes.

Mr. Chadwick found six species in the material submitted to

¹ Reports on the Marine Biology of the Sudanese Red Sea.—VII. "The Crinoidea." By Herbert C. Chadwick, A. L. S., Curator of the Port Erin Biological Station. Journ. Linn. Soc. (Zool.), vol. 31, pp. 44-47.

him, representing only two families, the Himerometridæ and the Antedonidæ, in the former the genera *Oligometra*, *Stephanometra*, *Dichrometra* and *Heterometra*, and in the latter *Iridometra*. All of these genera range throughout the East Indian region, and are characteristic littoral types of that area.

The first crinoids known from the Red Sea were *Tropiometra carinata* and *Heterometra savignii*, both of which were well figured by Savigny in his "Description de l'Egypt" in 1817, the former identified by Audouin as "Comatula sp.," the latter as "Comatula multiradiata." There is no further reference to the first of these figures; but de Blainville in 1836 copied the second in the atlas to his "Manuel d'Actinologie"; in doing this he made a curious mistake, for the plate is lettered "Comatula adeona" though in the text the description of *Comatula adeona* is taken from Lamarck, and the species is stated to have ten arms. In the following year the "Penny Encyclopedia" copied de Blainville's account of *Comatula adeona*, multiradiate figure and all, and the same slip was made by the "Natural History" of Knight published in 1867.

Rüppel, in the course of his travels, found in the Red Sea an interesting multiradiate comatulid upon which he bestowed the MS. name of *Comatula cucomelas*, but he does not appear to have mentioned it anywhere in his works. In 1833 Leuckart came across his specimens in the Senckenburg Museum, and published the name, together with the locality, though without any diagnosis.

In 1841 Professor Johannes Müller described his *Alecto savignii*, based upon specimens which had been brought from the Red Sea by Hempricht and Ehrenberg, and he also identified the *Comatula multiradiata* of Audouin, figured by Savigny, as this species. In 1869 von Martens recorded Müller's *Alecto palmata*, which had been originally described from India, from the Red Sea, though he apparently did not know that this was the same form as that recorded as *Comatula leucomelas* by Leuckart in 1833.

Nothing more was recorded regarding Red Sea comatulids for some time; Moseley analyzed the coloring matter from an unidentified species from Suez (possibly *Oligometra serripinna*), and Ludwig in 1880 listed two of the species known from that locality, but omitted the third. Carpenter, in the "Challenger" report was unable to add anything, though he increased the known range of *Heterometra savignii* by recording it from Muscat and

Kurrachee. In 1890 Dr. Hartlaub described *Dichrometra klunzingeri* from Koseir, and identified the *Comatula leucomelas* of Rüppel with the *Alecto palmata* of Professor Müller.

Mr. Chadwick did not find *Tropiometra carinata* nor *Dichrometra klunzingeri* in the collection examined by him, but he did find the other two species known from the Red Sea, *Heterometra savignii* and *Dichrometra palmata*; the remaining four species recorded include one family and three genera new to the region; they are, *Oligometra serripinna*, *Iridometra parvicirra*, *Stephanometra marginata* and *Dichrometra protectus*.

Oligometra serripinna is recorded from Suez Bay, where it was dredged at a depth of 10 fathoms; the specimens differ from the type in the greater number of cirrus joints, and, in view of the general constancy of the cirrus characters in this genus, may eventually turn out to be a recognizable form, as may also those recorded under the same name from Ceylon; correlated, as usual, with the more numerous cirrus joints, the lower pinnules have also more numerous joints.

Iridometra parvicirra, discovered by the "Challenger" among the Philippine Islands, is recorded from ten fathoms in Suez Bay. The single specimen has a large number of cirrus joints for the genus, which, together with the furrowed first primibrach, would suggest that it was rather closer to the *I. nana* group of species than to *I. parvicirra*; the former occur from Mauritius to Japan, while the latter were previously known from the Philippines and Japan.

We share the author's doubt in regard to his identification of *Stephanometra marginata*, which he records from Suez Bay, in ten fathoms.

Dichrometra protectus (under the later name *imparipinna*) is given from Suez Bay, and Suakim. The number of arms in the specimens is unusually small, and it would have been well worth while to have recorded their size. In addition to the localities cited by Mr. Chadwick, the species is known from Cebu, Philippines, Fiji and Singapore.

Dichrometra palmata was found on the coral reef at Misharif Island, Khor Dongola, and from between tide marks at Suez.

Heterometra savignii (emended, following Carpenter, to *savignyi*) is recorded from four fathoms in Suez Bay, from nine fathoms at Ul Shubuk, from ten to twelve fathoms at Khor Shinab, and at the anchorage at Salaka; the distribution of the species is given as "Red Sea, Ceylon," but I am unable to recall any record from the latter place; Carpenter gives it from

as far east as Kurrachee, and says that it "is not known to extend further eastwards," and I know of no subsequent additions to its range; Mr. Chadwick did not give it from Ceylon in his list of the crinoids of that island published in 1904.

In the introductory paragraph Mr. Chadwick mentions the interesting fact that none of the Comasteridæ are known from the Red Sea. They probably occur there, however, and will eventually be discovered when more extended work is undertaken. The absence of any species of Zygometridæ is noteworthy, and also that of Himerometra, one species of which, *H. persica*, was first described from the Persian Gulf and subsequently found in the Philippines. He also takes occasion to point out a weakness in Dr. F. A. Bather's argument for the treatment of a syzygial pair of brachials as two single brachials united by syzygy, instead of a single brachial "with a syzygy," the treatment adopted by Carpenter and Hartlaub. Mr. Chadwick's contention is that if the two brachials united by syzygy were originally, as urged by Dr. Bather, united by the ordinary oblique muscular articulation of the distal portion of the arm, which oblique muscular articulation had been transformed into a syzygy at the same time dropping its pinnule, the pinnule upon the resultant epizygial would be upon the same side as that upon the joint preceding the hypozygal, instead of on the opposite side, as is always the case. Mr. Chadwick is inclined to believe that this is evidence in favor of the views of Hartlaub and Carpenter, and against the ideas of Dr. Bather. I maintain that the syzygial pair is the morphological equivalent, not of one joint, as urged by Carpenter (in part) and Hartlaub, nor of two joints as supposed by Dr. Bather and apparently considered by Professor Perrier, but of *three* joints, the central one of which has dwindled and disappeared, so that the oblique muscular articulations on its proximal and distal ends have become superposed, their ligaments, being dominant over their muscles, fusing and forming the radiating figure which is the original of the later more perfected syzygy, while the muscles, and with them the pinnule sockets (borne by the muscular fossæ) have disappeared. Thus the syzygy originally, instead of having a single pinnule, as supposed by Dr. Bather, had two, which neutralized each other, so that the syzygy in its perfected form has no effect on the pinnulation.

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WASHINGTON, D. C.,
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